The influence of an external magnetic field on the spinose planktonic foraminifer *Globigerinoides ruber*

Master's thesis

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submitted by

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Contents

1 List of abbreviations

Chi^2	Chi-squared test statistics
CI	Confidence intervall
DF	Degrees of freedom
F	F-ratio
μ	Micro
N	Sampling size
n	Nano
nb	Number
p	Probability value
R^2	Coefficient of determination
SD	Standard deviation
T	Tesla (SI unit for the magnetic field strength)
x	Explanatory variable
y	Response variable

2 Abstract

The planktonic foraminifer *Globigerinoides ruber* shows a semilunar gametogenesis cycle. It has been proposed that the changes of the Earth's magnetic field during full and new moon (in the order of ∼10 - 100 nT) are the trigger for their simultaneous gamete release, yet no experiments have been conducted to test this hypothesis. In my MSc research project I carried out an experiment using an external magnetic field of roughly the same strength as the Earth's magnetic field (∼ 69 μT, Earth's magnetic field: ∼ 50 μT) to see whether this magnetic field acts as a trigger for simultaneous gametogenesis in *G. ruber*.

All experiments were performed aboard the research vessle *Maria S. Merian* (MSM58, 09/09 - 07/10/2016, from Reykjavík (Iceland) to Ponta Delgada (Azores, Portugal)) under constant light and temperature conditions. Foraminifera in the treatment group were exposed to the additional magnetic field, while control specimens were kept without an additional external magnetic field.

A shift to earlier gametogenesis was detected for foraminifera under treatment. I thus propose that simultaneous foraminiferal gametogenesis can be triggered by an external magnetic field, supporting the theory that the Earth's magnetic field changes over the lunar cycle act as a trigger for synchronizing gametogenesis. It has to be tested whether magnetic field changes in the order of the changes over the lunar cycle (∼ 10 to 100 nT) can act as a trigger, too, and what the mechanisms behind detecting magnetic field changes is.

Moreover, differences between foraminifera caught north, south and within the Azores Current were found. Fewer foraminifera from the southern stations underwent gametogenesis than from the other groups. It needs to be tested whether these differences could be caused by differences within the haplotype or by phenotypic plasticity and whether foraminifera north, south and within the Azores Current are different populations, subspecies or even cryptic species.

The suggested reactions on the gametogenesis of *G. ruber* due to changes of the Earth's magnetic field could also account for simultaneous gametogenesis events in other foraminiferal species and planktonic organisms.

3 Introduction

Many planktonic organisms show a simultaneous gamete release, for example foraminifera (Spindler et al., 1979), marine worms (Friedlaender, 1898) and corals (Harrison et al., 1984). In the vast pelagic zone, simultaneous gamete release is proposed to increase the probability of gamete fusion and thus of successful reproduction (Jonkers et al., 2015). The simultaneousness of the gamete release is either triggered by external signals (e.g. moonlight, Hauenschild, 1956) or maintained by an endogeneous biological clock through internal signals (e.g. melatonin in mammals, Armstrong, 1989) (Raible et al., 2017). One often suggested trigger for different species is the lunar periodicity. There are many examples of this periodicity, such as the palolo worm (*Palola viridis*). Once a year, the worms rise to the surface for a massive reproduction event (Gray, 1847). Other planktonic species showing lunar or semilunar reproduction cycles are planktonic foraminifera (Spindler et al., 1979), tropical corals (Harrison et al., 1984), sea urchins (Fox, 1922) and fish (Takemura et al., 2010). Possible triggers for these reproduction events are changes in the moon light (Bentley et al., 1999), the Earth's gravity (Taki, 1949) or the Earth's magnetic field strength (Bijma et al., 1990a).

3.1 Influence of the Earth's magnetic field on organisms

Many organisms are influenced by the Earth's magnetic field. The best known example is given by migratory birds, who use the Earth's magnetic field for orientation (e.g. Wiltschko and Merkel, 1966). But also young loggerhead turtles use the local Earth's magnetic field as a guidance for their migratory pathway (Lohmann et al., 2001), cattle seem to orient their body axes along the north-south axis (Begall et al., 2008) and for insects the Earth's magnetic field seems to have an impact on the reproduction time (Wan et al., 2014). As to the cause of the synchronisation of gametogenesis to the lunar cycle there is still a considerable degree of uncertainty (Jonkers et al., 2015). Different lunar rhythms support different hypotheses about possible external triggers for the lunar periodicity. The trigger behind a full lunar periodicity could be the change of the moon light over the lunar cycle. For a semilunar periodicity, however, changes of either gravity or the Earth's magnetic field are a more likely trigger. During both full and new moon, the moon stands in one line with the sun, thus the lunar influence on gravity, tides and the Earth's magnetic field is roughly the same during full and new moon (Newton, 1687). The light intensity, however, is very different for full and new moon.
First evidence was found that the moonlight can serve as a zeitgeber for the polychaet *Platynereis dumerilli* (Hauenschild, 1956). There have also been some experiments on the foraminifer *Hastigerina pelagica* by Spindler et al. (unpublished data), where the effect of light as a trigger for simultaneous gametogenesis was tested and it was found that the majority of *H. pelagica* underwent gametogenesis after four light-dark cycles after full moon. However, there have been no studies about the influence of the tidally, and thus lunary, induced changes of the Earth's magnetic field on simultaneous spawning events, which have been proposed as a zeitgeber for simultaneous gamete release in some planktonic foraminifera (Bijma et al., 1990a).

3.2 The Earth's magnetic field

The average intensity of the Earth's magnetic field on the Earth's surface is approximately 50 μT (Merrill and McElhinny, 1983). The Earth's core works as a geodynamo: a freely developing flow of the electrically conducting fluid of the Earth's core is creating an electric field, which, according to

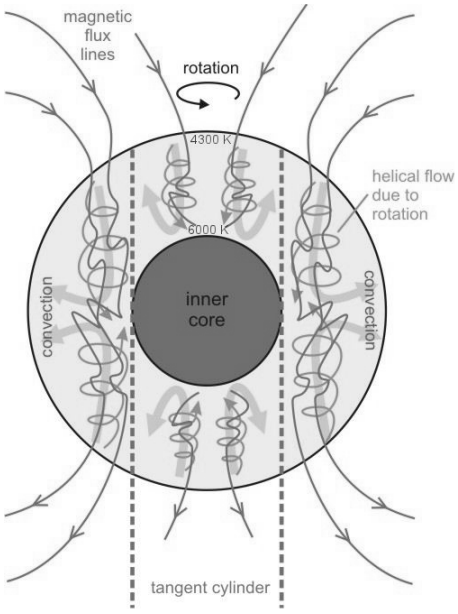


Figure 1: Origin of the Earth's magnetic field.
A combination of the Earth's rotating inner cores and convection currents of the fluid outer part causes the Earth's magnetic field.

the Ampères law, is encircled by a magnetic field and gets self amplified (Fig. 1). The solidification of the inner iron core provides the energy for the geodynamo. (Müller and Stieglitz, 2000). Due to the declination of the Earth's magnetic field, the magnetic field strength increases with the latitude (Fig. 2, Lilley and Day, 1993). As seawater consists of charged particles, the tidal movements cause an electric current, which also forms a magnetic field (Osgood et al., 1970). This magnetic field influences the Earth's magnetic field in an order of $\sim$ 10 - 100 nT (personal communication, Prof. Dr. Winklhofer). The tidal influence on the Earth's magnetic field is highest during spring tides, which occur at full and new moon (Newton, 1687).

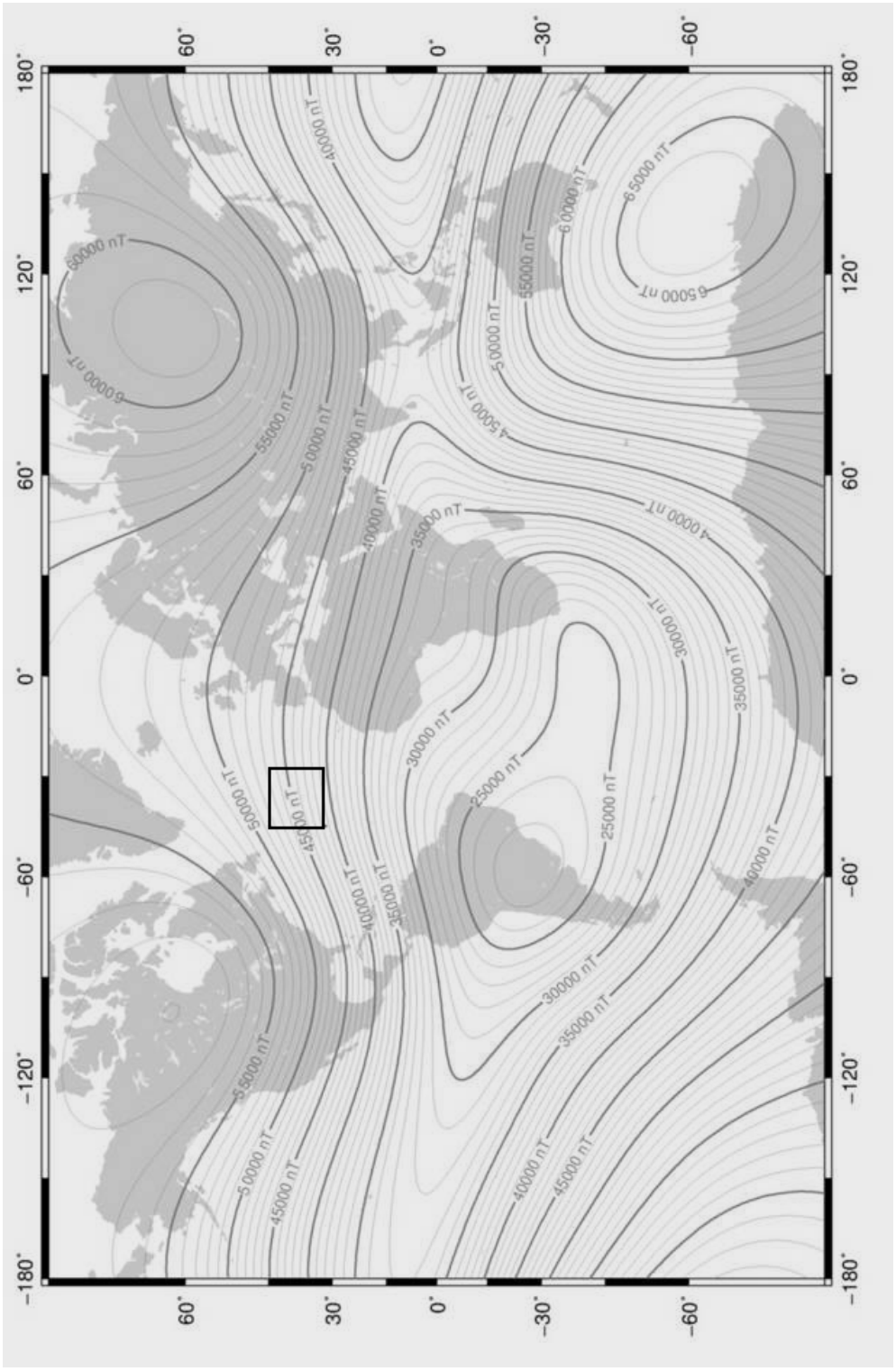
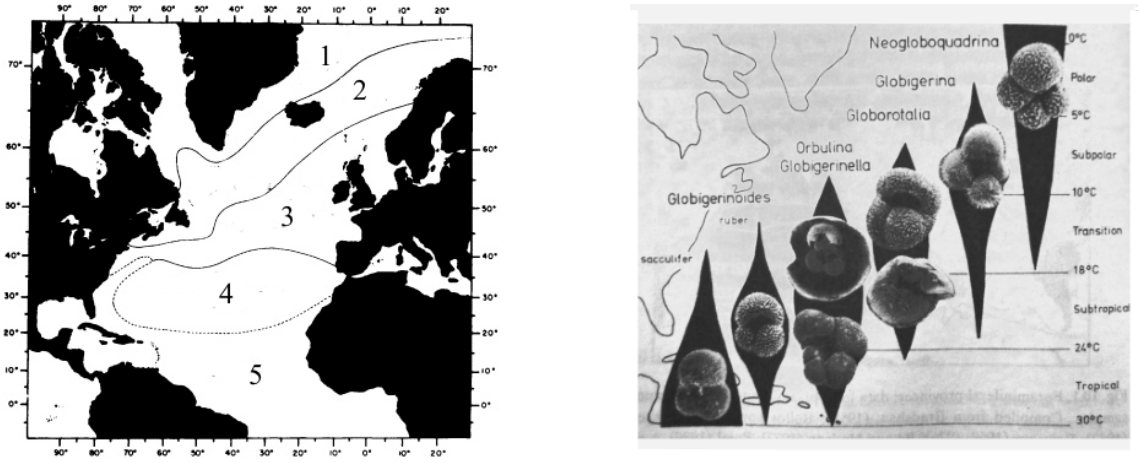


Figure 2: The Earth's magnetic field strength across the globe. The working area is indicated.



(a) (b)

Figure 3: Distribution of foraminifera
a) Foraminifera occur in all major oceanic provinces of the ocean, here shown for the North Atlantic. 1 = Arctic, 2 = Subarctic, 3 = Transitional, 4 = Subtropical, 5 = Tropical (after Tolderlund and Bé, 1971), b) Distribution of major Foraminifera in the North Atlantic (Hemleben et al., 2012).

3.3 Foraminifera

Foraminifera are unicellular organisms with approximately 10.000 recent species (Vickerman, 1992). They have been traditionally grouped into the taxonomic phylum of the Protista (Rigaud et al., 2013), however, molecular phylogenetic studies have led to a new hierarchical system, grouping foraminifera into a rank of the new group "Rhizaria" (Adl et al., 2005). Foraminiferal tests (their shells) can be organic walled, agglutinated, calcareous or siliceous (Hemleben et al., 2012). The majority of foraminifera are marine, however, there are some terrestrial (Lejzerowicz et al., 2010) and freshwater species (Pawlowski and Holzmann, 2002). Except the freshwater genus *Reticulomyxa*, all foraminifera build a test, which usually consists of multiple chambers (Pawlowski et al., 1999), and have granuloreticulopodia, granular structured pseudopodia which can be extruded through an aperture. Of the marine foraminifera only the group of Globigerinida, containing approximately 50 species, is planktonic, the vast majority are benthic (Hemleben et al., 2012).
In Geology, foraminiferal tests are used as tracers. On the one hand, the tests as such, revealing species occurrence in the region of interest, can serve as an indicator for temperature and climate conditions (Hemleben et al., 2012). This technique is based on indicator species and uses the direct observation of the tests (Kucera, 2007). On the other hand, trace elemental and stable isotopic compositions of the test can serve as tracers for water temperature (δ^{18}O (Emiliani, 1955) and Mg/Ca ratio (Nürnberg et al., 1996)) and other climate conditions of interest, e.g. carbonate system parameters (U/Ca ratio (Keul et al., 2013)).

3.4 Planktonic foraminifera

Planktonic foraminifera are ubiquitous, surface dwelling, oceanic species (Hemleben et al., 2012). Schiebel and Hemleben (2005) subdivide planktonic foraminifera into 5 informal morphogroups:

1. spinose (Globigerinoidea)
2. non-spinose (Globorotaloidea)
3. non-spinose microperforate (Heterohelicoidea)
4. microperforate species other than Heterohelicoidea
5. monolamellar Hastigerinidae

The first description was given by d'Orbigny in 1826. Planktonic foraminifera occur in all oceanic provinces with each oceanic province having its own marker species (Fig. 3). There is some evidence that cryptic speciation takes place in planktonic foraminifera, following the major ocean current systems. Three cryptic species of *Orbulina universa*, isolated by the hydrography, have been found in the Atlantic ocean (de Vargas et al., 1999).
The cellular organization of foraminifera is variable, as the cytoplasm shows a high streaming activity. Since the cytoplasm can stretch out of of the test, cell organelles can lie inside or outside of the test (e.g. mitochondria can be found in the pseudopodial network, Hemleben et al., 2012). Foraminifera contain typical eukaryotic cell organelles (Schiebel and Hemleben, 2005) and can be bilobate, which means that their nucleus spreads over two chambers; a thin strand connects both parts over the septal aperture (Hemleben et al., 2012). Planktonic foraminifera contain fibrillar bodies, which have been proposed to be either calcification organelles (Spero, 1988) or floating devices (Hemleben et al., 2012). An aperture connects the foraminifer to the exterior, chambers are connected via a foramen. Gas exchange takes place through pores and the apertures (Schiebel and Hemleben, 2005). The spines of *Globigerinoidea* are thought to provide structure for the rhizopodial network outside the shell for food capturing (Hemleben et al., 2012).
New chambers are formed by calcite precipitation along a previously excreted primary organic layer. Two different models have been proposed about the uptake of the calcium for calcification in foraminifera:

1. Endocytosis of sea water with vacuoles transporting dissolved calcium towards the site of calcification (Erez, 2003).
2. Trans-membrane transport of calcium (Nehrke et al., 2013).

About 10% of all (benthic and planktonic) foraminifera carry symbionts which are commonly dinoflagellates or chrysophycophytes (Lee and Anderson, 1991). They contribute compounds from photosynthesis and may even provide energy for calcification processes (Schiebel and Hemleben, 2005). The majority of planktonic foraminifera are omnivorous, however, they tend to mainly feed on zooplankton, like copepods, but diatoms and dinoflagellates are also a common prey. For some non-spinose foraminifera cannibalism has been reported, however, they show a higher tendency towards herbivory (Hemleben et al., 2012). They are preyed on by macrozooplankton and nekton (Bradbury et al., 1970).
In contrast to benthic foraminifera, planktonic foraminifera seem to only reproduce sexually (Schiebel and Hemleben, 2005), gamete release was first described by Rhumbler (1911). Due

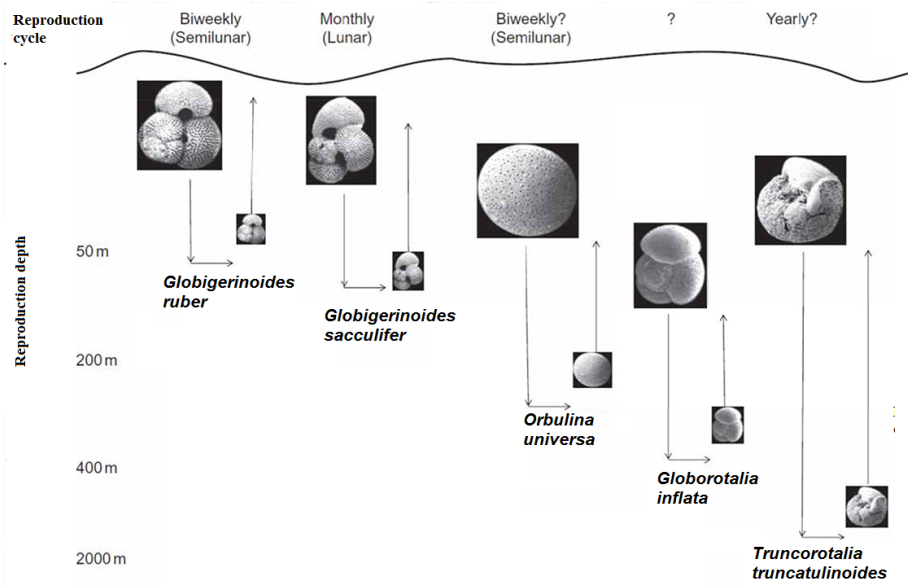
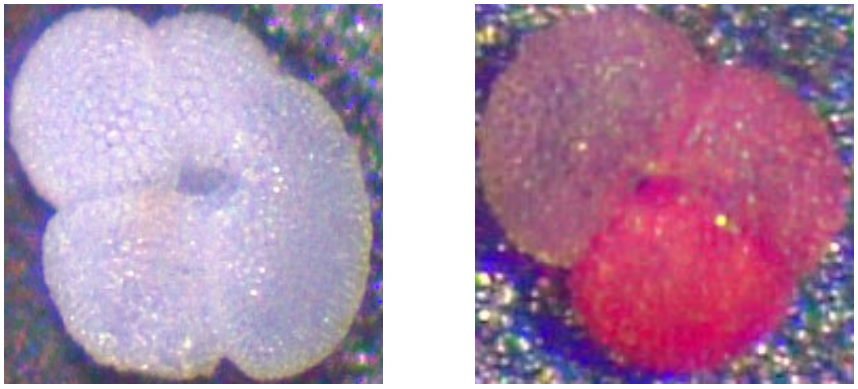


Figure 4: Life cycle of some planktonic foraminifera.
Different species of foraminifera undergo gametogenesis within different water depths and time periods. Gametogenesis takes place in deeper water levels than adult foraminifera usually occur (BouDagher-Fadel, 2005, after Hemleben et al., 2012).

to the vastness of the marine planktonic environment, different adaptations ensure sufficient reproduction rates: motile gametes with sufficient food reserves, as well as synchronized gamete release (Hemleben et al., 2012). Usually, the gamete release is depth-specific, which means that during gametogenesis the buoyancy changes (Fig. 4). An adult foraminifer releases about 200,000 to 400,000 gametes (Schiebel and Hemleben, 2005). The simultaneous reproduction of foraminifera can influence the carbon fluctuations, e.g. in the equatorial oceans (Kawahata et al., 2002). After gamete release, only the empty shell, without spines, remains for most species (Hemleben et al., 2012). The rhythm of simultaneous gamete release is in many cases of shallow dwelling foraminifera the synodic lunar cycle (e.g. Spindler et al., 1979). Gametogenesis takes place either every two weeks (semilunar cycle, e.g. *Globigerinoides ruber*) or every four weeks (lunar cycle, *Globigerinoides sacculifer*). For the species *Truncorotalia truncatulinoides* reproduction events might happen only once a year (Fig. 4). Until now, the cause of the synchronization of gametogenesis to the lunar cycle has not clearly been found (Jonkers et al., 2015). There have only been a few experiments about possible light triggers (Spindler et al. unpublished), which indicated that gametogenesis in *Hastigerina pelagica* took place four light-dark-cycles after full moon, but the effect of lunar induced magnetic field changes on foraminiferal gametogenesis has not been tested so far.

3.5 *Globigerinoides ruber*

G. ruber (d'Orbigny 1839), the species used in experiments described in this thesis, is a planktonic foraminifer, bearing autotrophic dinoflagellates as symbionts. Two distinct varieties of the species have been described: one showing a white (*G. ruber* (white)) and one showing a pink (*G. ruber* (pink)) pigmentation (Fig. 5 Hemleben et al., 2012).
G. ruber (pink) was found to be calcifying in warmer waters than the white variety, which suggests that they have slightly different ecological niches (Richey et al., 2012) and also prefer warmer



(a) (b)

Figure 5: Different varieties of *G. ruber*, their size is $\sim$ 250 μm.
a) *G. ruber* (white), b) *G. ruber* (pink)

habitats than *G. ruber* (white) (Be and Hamlin, 1967). Both varieties are most abundant in tropical and subtropical waters (Fraile et al., 2008). Their temperature tolerance lies between 14 - 32°C, the salinity tolerance between 22 - 49 (Bijma et al., 1990b). White *G. ruber* are the most common species in the Azores Front system (Schiebel et al., 2002), where sampling took place, with their highest abundance from September to May (Storz et al., 2009). *G. ruber* undergoes gametogenesis in a semilunar cycle (Bijma et al., 1990a). The idea that the semilunarity is caused by internal zeigebers was excluded as the semilunarity of the gametogenesis in *G. ruber* was not observed under laboratory conditions, which suggests that an external trigger is needed to maintain the semilunar reproduction cycle (Bijma et al., 1990a). The semilunarity of gametogenesis in *G. ruber* makes it a great study organism to test the effect of changes in the Earth's magnetic field on gametogenesis, as the changes of the Earth's magnetic field are roughly the same at new and full moon (Thurman and Burton, 1997), whereas the light intensity differs for full and new moon.

3.6 The Azores Current region

The Azores Current is the eastwards flowing, northern border of the North Atlantic Subtropiocal Gyre (Stramma and Müller, 1989) and is related to the thermohaline Azores Front system (Gould, 1985). It meanders roughly between 30°and 45°N (Lázaro et al., 2013), transports about 10 - 12x106 m^3 sec^{-1} and has a speed of up to 40 cm sec $^{-1}$ (Gould, 1985). The mean surface temperature of the stations where the samples have been taken lies at 24°C $\pm$ 1°C (SD) and the salinity at 36.4 $\pm$ 0.24 (SD) (Fig. 6). In total, sea surface temperature varies from 17 - 25°C over the year.

3.7 Hypotheses

The aim of this thesis is to analyze, whether an external magnetic field has an observable effect on the gametogenesis of *G. ruber*. My hypotheses are:

H 1.

The lunar phase (defined as the day of full/ new moon plus four days) has an effect on whether or not a foraminifer undergoes gametogenesis.

H 2.

In the control group, more foraminifera undergo gametogenesis within the lunar phase, in the treatment group more foraminifera undergo gametogenesis outside of the lunar phase.

H 3.

The health of foraminifera is not affected by the experiment or the conditions they were caught under.

1. The number of days until death (counted from the day a foraminifer was set into the experiment), as well as the date of death, is not different between control and treatment.
2. Uncontrolled explanatory factors (e.g. colour variety of the foraminifer and the conditions a foraminifer was caught under) neither affect the number of days until death, nor the date on which a foraminifer dies without undergoing gametogenesis.

H 4.

Treatment and control group differ from one another: the external magnetic field shows an effect on:

1. Whether or not a foraminifer undergoes gametogenesis.
2. The number of days until gametogenesis (beginning on the day a foraminifer was set into the experiment).
3. The date on which foraminifera undergo gametogenesis.

H 5.

Uncontrolled explanatory factors (e.g. colour variety of the foraminifer and the conditions a foraminifer was caught under) have an effect on:

1. The number of days until foraminifera undergo gametogenesis.
2. Whether or not a foraminifer undergoes gametogenesis.
3. The date on which foraminifera undergo gametogenesis.
4. Whether or not gametogenesis of the foraminifer lies within the lunar phase.

H 6.

Interactions between controlled and uncontrolled explanatory variables have an effect on whether or not foraminifera undergo gametgoenensis.

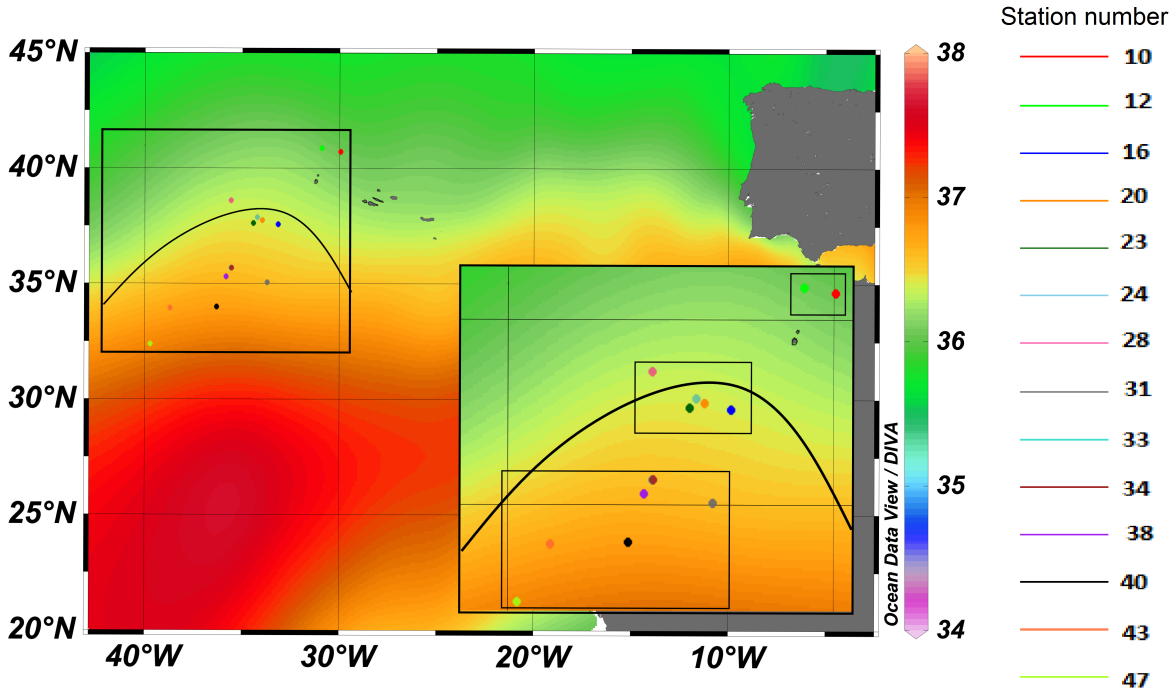
H 7.

The floating behaviour is influenced by:

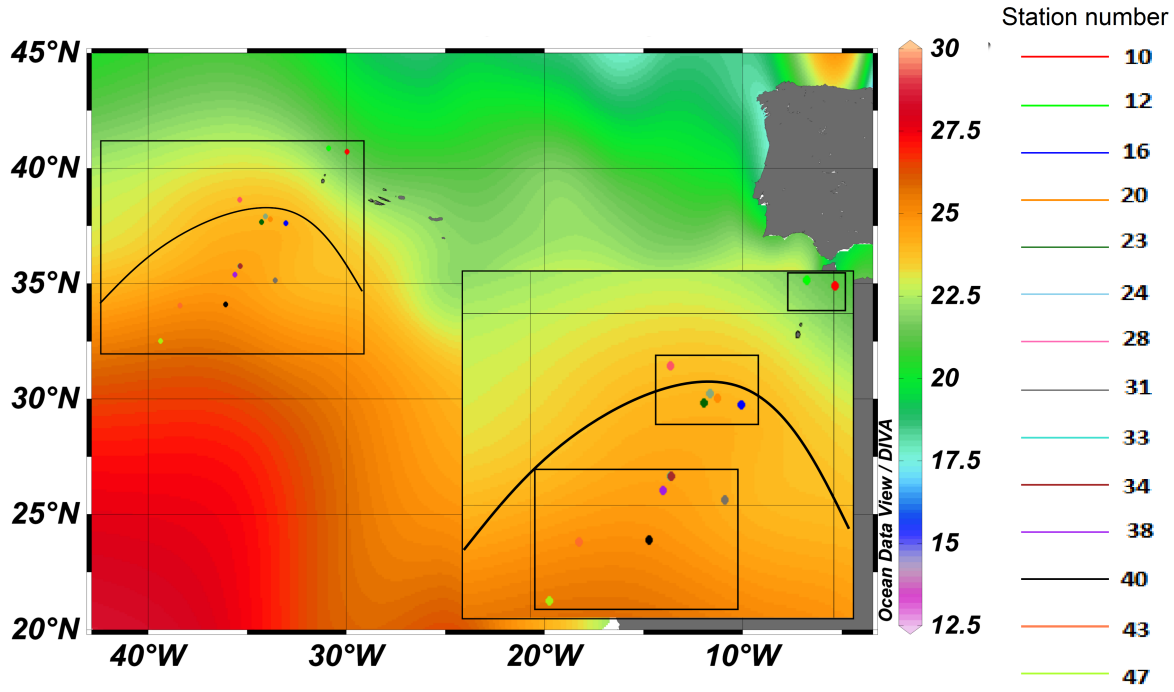
1. The experiment.
2. The lunar phase.

H 8.

Foraminifera for which floating behaviour is observed are more likely to undergo gametogenesis.



(a)



(b)

Figure 6: Maps of the Azores Current region:
a) Salinity, b) Temperature. The stations where foraminifera used in this experiment were caught are marked. Boxes indicate the current dependent grouping for statistical analysis. The black line shows the course of the Azores Current, using the salinity and temperature data. Maps were generated in odv (Schlitzer, 2008), courtesy of N. Keul.

4 Material and Methods

4.1 Experiments

All experiments were conducted during the MSM58 cruise (RV *Maria Sybilla Merian*, 09/09 - 07/10/2016) from Reykjavík (Iceland) to Ponta Delgada (Azores, Portugal) (Fig. 7). Culturing took place between the 18/09 and the 05/10/2016 (17 days).

4.1.1 Culturing

For sampling, a hand held plankton net (aperture: 25 cm, mesh width: 200 μm) was used. The net was tied to a 10 m rope and was hauled over the rail. Depending on the current and wave situation, the rope was either tied to a cleat or held in hand whilst walking up and down the deck. The duration of the hand net hauls depended on the plankton density in the sampled area, usually the net was left out for a maximum of 10 minutes. Moreover, MultiNet samples were taken (from depths of 100 m and 700 m). However, as the concentration of foraminifera in the MultiNet hauls was too low, specimens for the experiment were solely taken from handnet hauls. Samples were taken all over the day and at all stations, however not all foraminifera were used for the experiment (control: Table 1, treatment: Table 2).
Foraminifera were picked under a stereo microscope (40 x magnification) from the plankton sample and were set into the experiment after at least one day under high light conditions for recreation. All cultures were kept in a temperature controlled room aboard the RV *Maria S. Merian* at 20°C. One aquarium lamp (30 cm long, 3 rows of LEDs) per setup in a distance of 1 m was used to mimick a 12 hours light/dark cycle (light intensity: 20.83 μmol m^{-2} s^{-1}, measured with an LI-250 A Light Meter from LiCor). The light conditions for foraminifera in the experiment were the same and kept constant over the time of the experiment to exclude light changes as a possible trigger for gametogenesis.
Foraminifera in culture were fed daily, mostly in the evening, with 1- to 2-day-old living Artemia (*Artemia* sp.), except when a foraminifer was still feeding, i.e. when it still had an Artemia in its spines. Artemia were pipetted into the spines of the foraminifer, using a glass pasteur pipette, dead free floating Artemia and Artemia carcasses were removed from the water. If a foraminifer could not be fed for at least two consecutive days, it was considered dead, as non-feeding foraminifera have most likely lost their cytoplasm and / or their spines. Dead foraminifera were removed and replaced after confirming their death using a stereo microscope (40 x magnification).

4.1.2 Experimental Setup

The experiment was set up in two large boxes (37 x 50 cm) which were fastened using ropes and tension belts: one for the control group and one for the treatment group. All foraminifera were kept in Schott bottles (100 mL), one specimen per bottle (Fig. 8 a). For the control group, bottles were arranged in rows. For the treatment group, bottles had to be arranged in the same distance to, thus in a circle around, a magnet of the required strength, to achieve an equal magnetic field strength for each foraminifer (Fig. 8 b and c). 4 magnets (2.5 cm high, 0.5 cm diameter, magnetisation: N45) were used to build a 10 cm high magnet, which was wrapped with ducktape to prevent the construction from breaking. The magnet-tower was fixed on the ground of the box using modelling clay. This also elevated the magnet to the height of the Schott-bottles. As the magnetic field lines are straightest whilst running parallel to the magnet (Fig. 8 c), elevating the magnet to

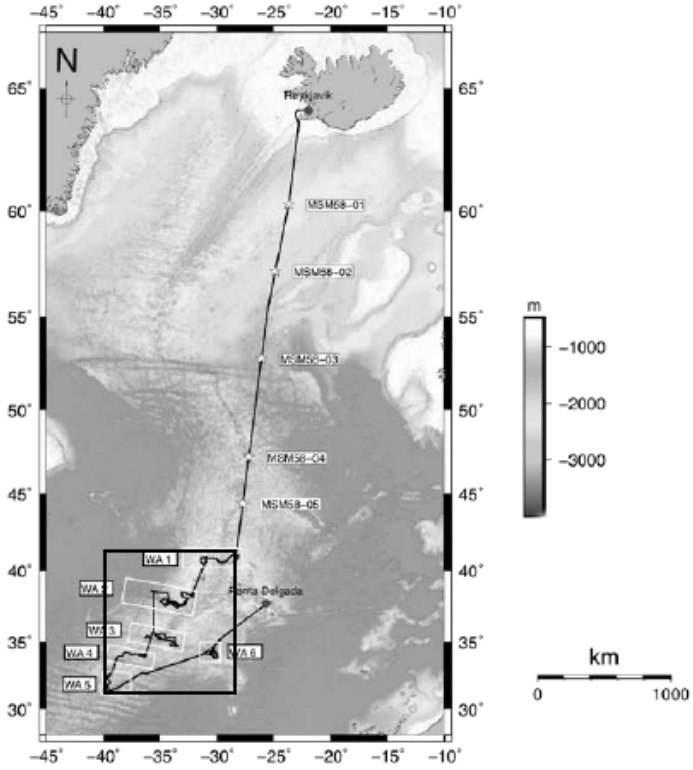
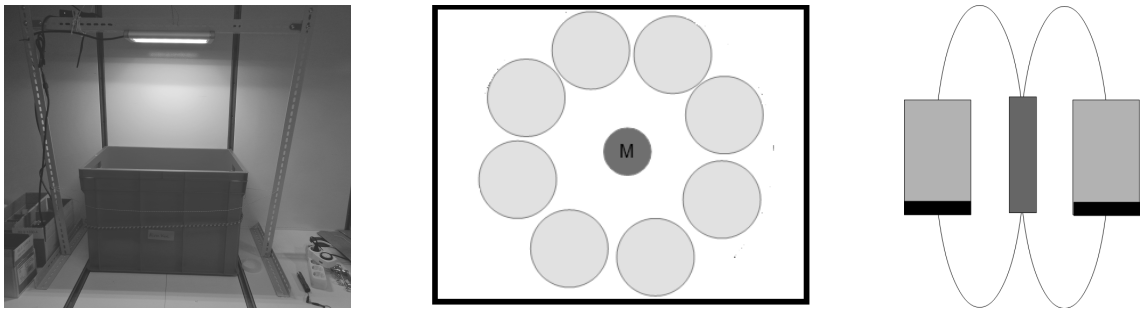


Figure 7: Cruise plan of the MSM58 cruise during which the experiments were conducted. The area where foraminifera used in this experiments come from is marked. (Repschläger, 2016)

the height of the bottles helped creating an equal magnetic field strength in the single bottles. The single bottles were placed in the same distance (6.75 cm) to the magnet, to ensure that they were all exposed to the same additional magnetic field strength of 69 μT ± 14 (SD)(mean drift of the magnetometer over the measuring time = 8 μT). The magnetic field strength was measured every day with a hand held three-axis-magnetometer for five random Schott-bottle positions per setup. The mean background magnetic field strength for foraminifera in the treatment was 44 μT ± 22 (SD), for the control group 45 μT ± 15 (SD), the mean drift of the magnetometer during measurements was ±8 μT.

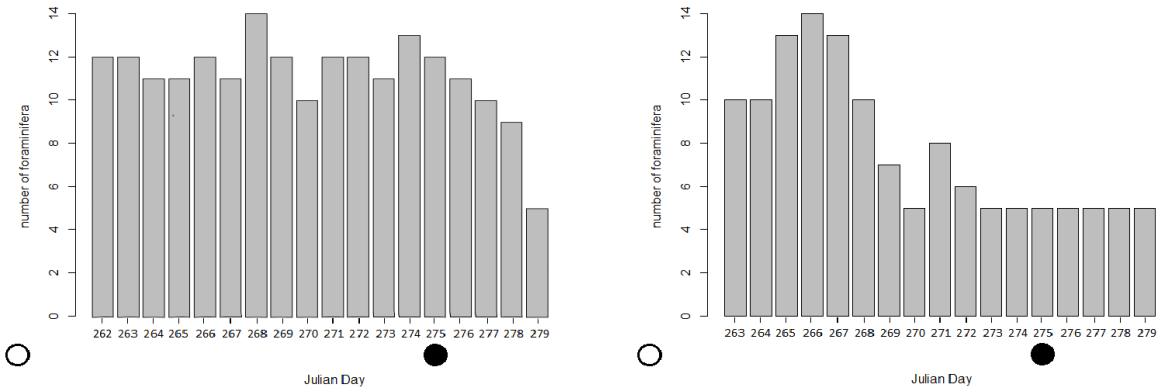
4.1.3 Measured parameters

The floating behaviour of foraminifera was analysed on a daily basis. For this, the position of a foraminifer in the bottle was noted, containing the vertical and horizontal (i. e. floating or not) location of the foraminifer. Gametogenesis was measured on a binary scale: it was noted whether or not a foraminifer underwent gametogenesis. As parameters for gametogenesis, both spine condition and colour were used. Only specimens without cytoplasm and spines were considered as having undergone gametogenesis. The lunar phase was defined as the day of full or new moon + 4 days, based on Bijma et al (1990), who report the lowest number of foraminifera in surface waters between 3 to 5 days after full/ new moon, indicating that in this time they undergo gametogenesis in deeper water layers (Fig. 4).



(a) (b) (c)

Figure 8: Experimental Setup:
a) From the side, b) From above, c) Detailed setup of the bottles and the magnet. M = Magnet. Schott bottles were arranged in a circle around the magnet. Aboard the ship, the experiment was set up inside plastic boxes, which were secured, light was provided by aquarium lamps in a distance of 1 m. The field lines of a magnet go in an ellipse from the north pole to the south pole of the magnet and are straightest whilst running parallel to the magnet. In the same distance to the magnet the field strength is the same.



(a) (b)

Figure 9: Number of foraminifera in culture over time:
a) Control, b) Treatment. Foraminifera in treatment conditions were exposed to an external magnetic field of the strength of $\sim 69\ \mu$T. Please note the difference in the x-axis scale: Foraminifera under control conditions were set into the experiment one day before foraminifera under treatment conditions. The experimental design was unbalanced. The full circle indicates the day of new moon, the empty one the day of full moon.

4.2 Statistical Methods

All statistics were performed using the R-Software, Version 0.99.486 (R Development Core Team, 2008). Packages used are:

arm (Gelman and Su, 2016)
car (Fox and Weisberg, 2011)
ggplot2 (Wickham, 2009)
lattice (Sarkar, 2008)
lme4 (Bates et al., 2015)
nlme (Pinheiro et al., 2017)
QuantPsyc (Fletcher, 2012)
rms (Harrell Jr, 2017)
sciplot (Morales et al., 2012)
survival(Therneau, 2015)
userfriendlyscience (Peters, 2017)

For binary response variables, logistic regression with a generalized linear model, using a binomial error distribution and a log link function was applied. Dispersion parameters were estimated using a quasibinomial distribution. Residuals were checked visually for homoscedasticity and normality. For all other data, normality was checked using the Shapiro-Wilks test of normality. Homogeneity of variances was tested using the Fligner-Killeen test. Influential data points were checked using Cook's distance plots. For sufficiently normally distributed data with categorial explanatory variables, ANOVAs were performed, for non-normal data Kruskal-Wallis-Tests were used. Post-hoc tests were only performed at significance level and if the explanatory variable had more than two levels, the Hochberg test from the *userfriendlyscience* package was used for data with homogeneous variances, otherwise the Games-Howell test was used. For continuous explanatory and response variables, linear regression models were used. The 0.05 sigfnificance level was applied.

Response variables (y) are:

1. The number of foraminifera which underwent gametogenesis per day
   (a) Ratio of foraminifera which underwent gametogenesis in control
   (b) Number of foraminifera which underwent gametogenesis in control
   (c) Ratio of foraminifera which underwent gametogenesis in treatment
   (d) Number of foraminifera which underwent gametogenesis in treatment
2. Whether or not a foraminifer underwent gametogenesis
3. The date on which foraminifera underwent gametogenesis
4. The date on which a foraminifer died
5. Whether or not gametogenesis of foraminifera took place during the lunar phase (full / new moon + 4 days)
6. The days it took until a foraminifer underwent gametogenesis, starting on the day on which the foraminifer was put into the experiment

7. The days it took until a foraminifer died, starting on the day on which the foraminifer was put into the experiment
8. The floating behaviour of foraminifera
9. The number of foraminifera which underwent gametogenesis after a certain number of days

Explanatory variables (x) are:

1. Experiment (treatment or control)
2. Lunar indicator for the day of gametogenesis
   (a) Binary variable for the lunar phase (does the day lie within the defined lunar phase (full / new moon + 4 days): yes or no)
   (b) Days after full/ new moon
   (c) Days until the end of the lunar phase, starting on the day on which foraminifera were put into the experiment
3. Colour variety of the foraminifer (pink or white)
4. Azores Current dependent grouping (Groups were defined optically by using the mean temperature and salinity distribution in the Azores Current region for the time of sampling, Fig. 6)
   (a) Salinity
   (b) Temperature
   (c) Latitude
   (d) Longitude
5. Days until death of the foraminifer
6. Date on which foraminifera underwent gametogenesis or died
7. Date on which the foraminifer was caught
8. Whether or not the foraminifer was caught during the lunar phase
9. Floating behaviour of the foraminifer
10. Days until gametogenesis (beginning on the day a foraminifer was set into the experiment)

The experimental design was unbalanced (Fig. 9) due to death of foraminifera and replacing them for an increase of the sampling size (N). Therefore, the ratio of foraminifera which underwent gametogenesis was calculated for each day using the following equation, where nb = number:

$$\text{Ratio} = \frac{\text{nb of foraminifera which underwent gametogenesis per day}}{\text{nb of foraminifera in experiment per day}} * 100 \quad (1)$$

All values were rounded to the nearest integer.

5 Results

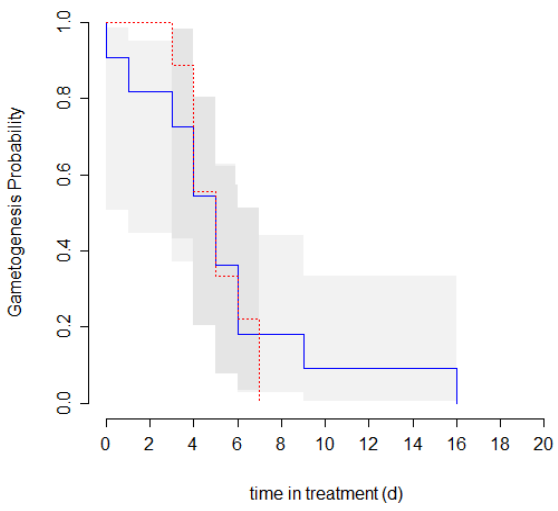
The influence of an external magnetic field on the gametogenesis of the foraminifer *G. ruber* was tested. A total of 113 foraminifera were cultured: 58 under control and 55 under treatment conditions. About 50% of the foraminifera in the experiment could not be used for analysis, as they were too broken to correctly identify and / or confirm whether or not they underwent gametogenesis. 55 foraminifera were used for analysis (control: 32, treatment: 23). In total, 41 foraminifera underwent gametogenesis (control: 23, treatment: 18) and 14 foraminifera died during the experiments (control : 9, treatment: 5). The mean survival time for all foraminifera was 5.1 days ± 3.1 (SD) (control: 5.2 days ± 3.7 (SD), treatment: 5.0 days ± 2.0 (SD)). Foraminifera came from different stations in the Azores region (Table 1, Table 2 and Fig. 6). The mean temperature foraminifera were taken from was 23.9°C ± 1.2°C (SD), the mean salinity 36.4 ± 0.2 (SD). According to the typical salinity and temperature distribution in September, the stations where foraminifera were sampled fell into the Azores Current at this season (Fig. 6). Stations were grouped according to their location with the Azores Current: north, south and within the current (Fig. 6).

Of the position data for each foraminifer per day, only the information whether or not it was floating (vertical position) could be used, as the Schott bottles were moved during the experiment and thus all other position definitions lacked a reference point.

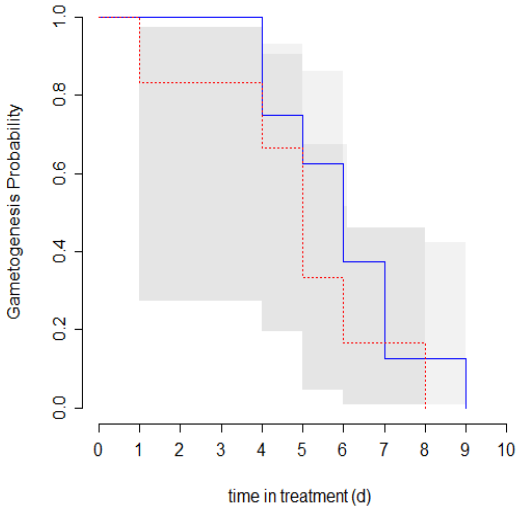
The magnetic field aboard, most likely created by electric devices, was measured for 5 bottles per day for each, treatment and control, and was not found to be significantly changing over time (mean: 44.8 μT ± 18.4 (SD), mean drift of the magnetometer over the measuring time = 8 μT, Table 4). The Earth's magnetic field and its global change was blocked out by the metal parts of the ship. The idea behind the experiments is that changes in the Earth's magnetic field might act as a trigger for gametogenesis of *G. ruber*.

All statistical data, separated for the model used, can be found in the appendix in tables 3 - 8. Dates are given in Julian days.

To gain a first impression on how the experiment influenced the gametogenesis probability for foraminifera, a Kaplan-Meier plot on data grouped according to their sampling position respective to the Azores Current, was made (Fig. 10). One can see that the probability for gametogenesis for foraminifera from two groups (caught north of and within the Azores Current) under treatment conditions decreases faster, indicating that they underwent gametogenesis earlier than foraminifera in the control.



(a)



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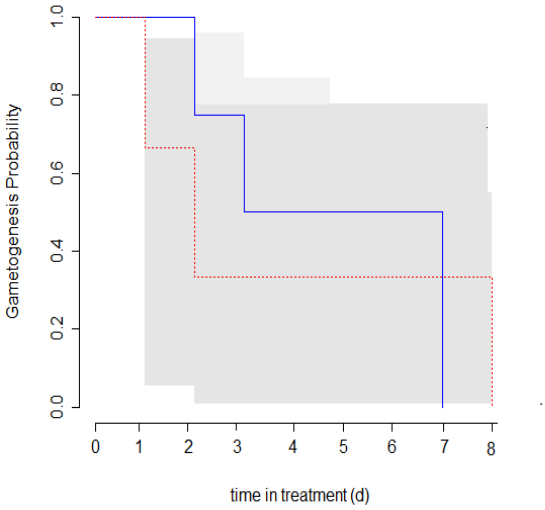


(c)

Figure 10: Kaplan-Meier plots showing the probability of foraminifera undergoing gametogenesis for the time in the experiment:
a) Foraminifera caught north of the Azores Current, b) Foraminifera caught within the Azores Current, c) Foraminifera caught south of the Azores Current, red = treatment, blue = control. Please note the difference in the x-axis scales. The shaded area gives the logarithmic conficdence interval. Foraminifera are separated depending on where they were caught relative to the Azores Current (Fig. 6).

5.1 Hypothesis 1

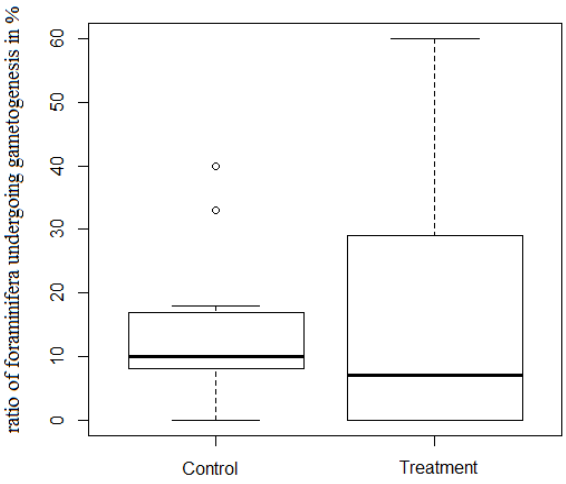
The lunar phase has an effect on whether or not a foraminifer undergoes gametogenesis.

The lunar phase had no effect on whether or not foraminifera underwent gametogenesis. However, the treatment affected whether or not foraminifera underwent gametogenesis during the lunar phase ($p = 0.040$, Table 3).

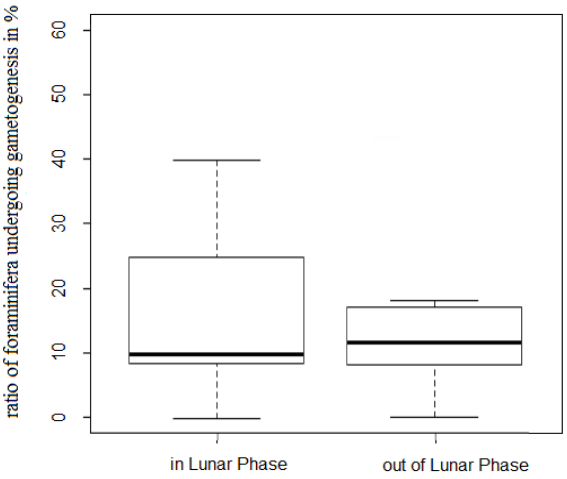
5.2 Hypothesis 2

In the control group, more foraminifera undergo gametogenesis within the lunar phase, in the treatment group more foraminifera undergo gametogenesis outside of the lunar phase.

The lunar phase had neither a significant impact on the ratio (explanatory 1 a), nor on the number of foraminifera undergoing gametogenesis (1 b) in the control group (1 a: $p = 0.268$, 1 b: $p = 0.773$, Fig. 11 b, Table 5). The same result was found using the days after full / new moon as an indicator for the lunar phase (1 a: $p = 0.534$, 1 b: 0.923, Fig. 12 c, Table 3).
However, the Gantt plot (Fig. 13 a) and the barplot of the ratio of foraminifera which underwent gametogenesis over time (Fig. 12 a) show a small peak of gametogenesis numbers within the lunar phase for the control group.
For foraminifera under treatment conditions a significant difference in the number of foraminifera which underwent gametogenesis was found within and outside of the lunar phase, using the binary coded factor for lunar phase ($p = 0.027$, Table 5), and a marginally significant difference was found using the days after full / new moon as an indicator for the lunar phase ($p = 0.067$, Fig. 12 d, Table 4). For the ratio of foraminifera which underwent gametogenesis, only the linear regression, using the days after full / new moon showed a significant effect (linear regression: $p = 0.034$, Fig. 12 b), whereas a Kruskal-Wallis Test, using the binary coded factor for the lunar phase, showed no significance ($p = 0.412$, Fig. 11 c). An accumulation of gametogenesis events outside of the lunar phase could be observed (Fig. 13 b). A logistic regression showed that the experiment did have a significant effect on whether or not gametogenesis took place within the lunar phase ($p = 0.040$, Table 3).



(a)



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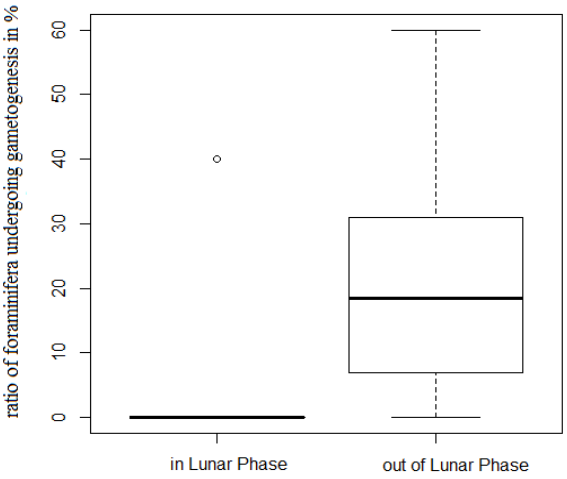
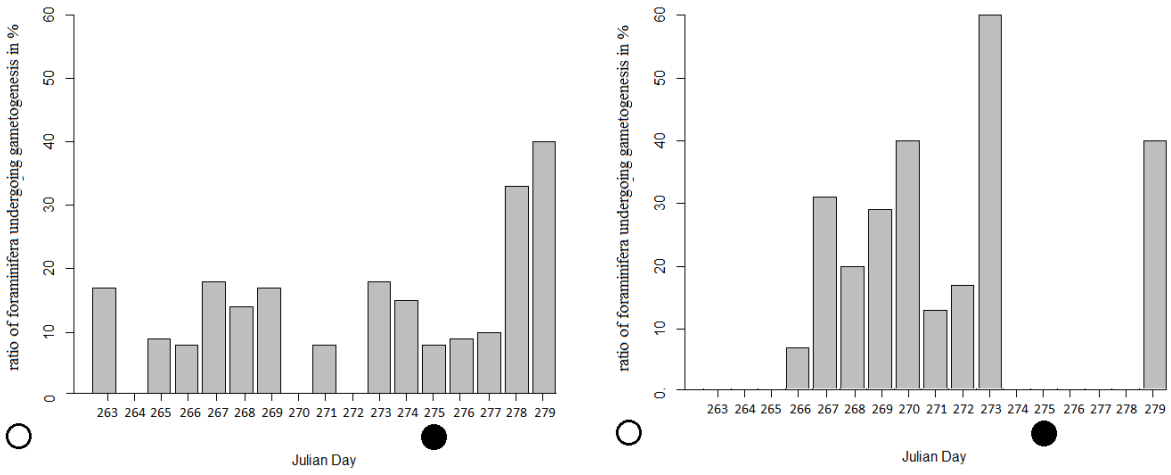


(c)

Figure 11: Comparison of the ratio of foraminifera which underwent gametogenesis:
a) In control and treatment, b) For control and c) For treatment within and out of the lunar phase. The line shows the mean, boxes represent the interquartile range, whiskers show the maximum and minimum value and dots show outliers.



(a)

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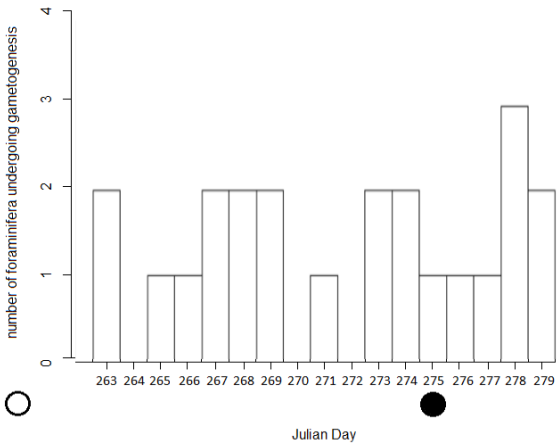
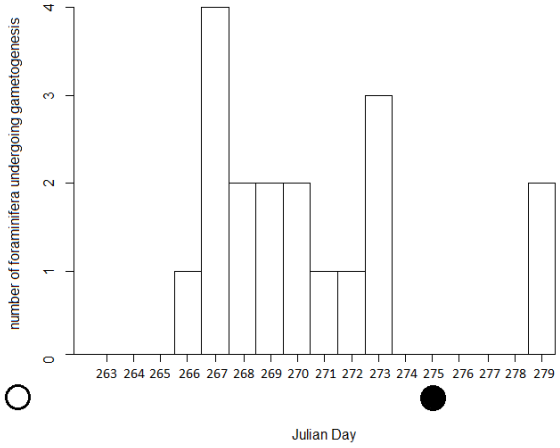
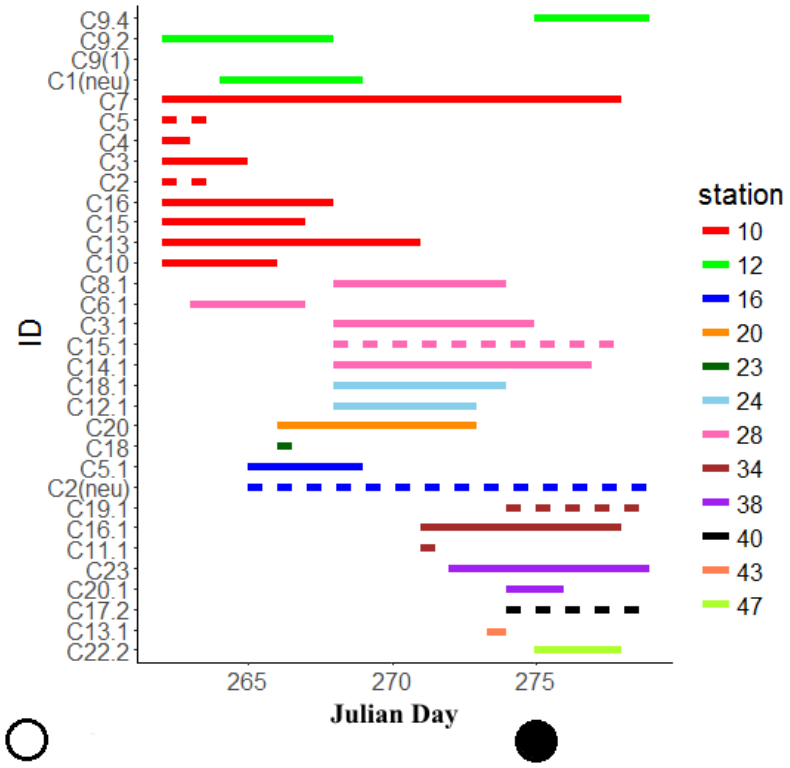


(c)

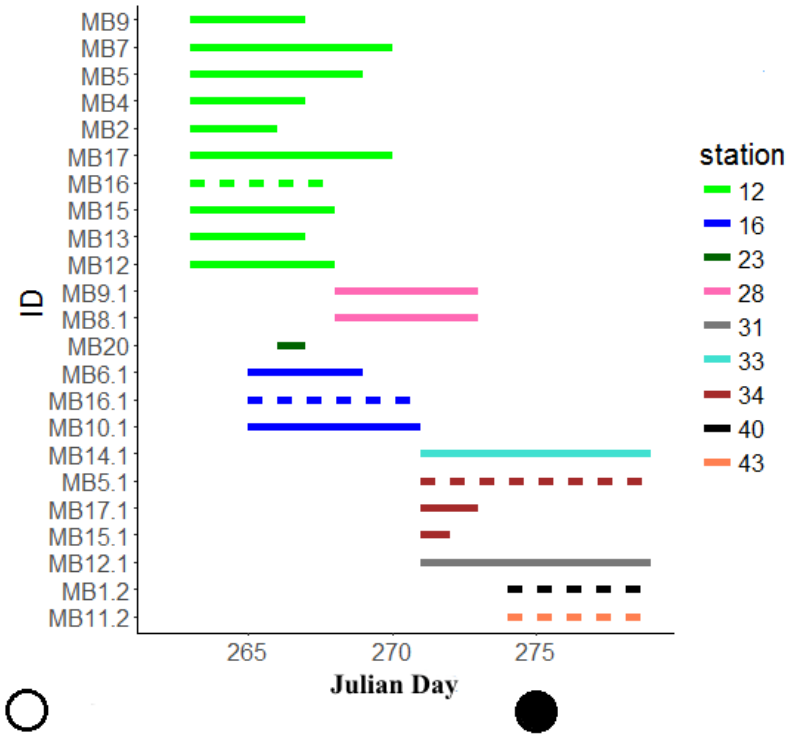


(d)

Figure 12: Comparison of the ratio and the number of foraminifera undergoing gametogenesis per day for treatment and control: left: Control, right: Treatment, upper row: Ratio of foraminifera which underwent gametogenesis per day (Equation 1), lower row: Number of foraminifera which underwent gametogenesis per day. The full circle indicates the day of new moon, the empty one the day of full moon.



(a)



(b)

Figure 13: Experimental duration for all foraminifera:
a) Control (C), b) Treatment (MB). Dashed lines represent foraminifera that died without undergoing gametogenesis. Colour indicates at which station a foraminifer was caught (see Fig. 6). The full circle indicates the day of new moon, the empty one the day of full moon.

5.3 Hypothesis 3

The health of foraminifera is not affected by the experiment or the conditions they were caught under.

1. The number of days until death, as well as the date of death, is not different between control and treatment.

   A Kruskal Wallis test showed no significant difference between the experiments for the date on which foraminifera died ($p = 0.194$, Table 6), an ANOVA showed no significant difference for the number of days until death between control and treatment ($p = 0.548$, Table 5).

2. Uncontrolled explanatory factors (e.g. colour variety of the foraminifer and the conditions a foraminifer was caught under) neither affect the number of days until death, nor the date on which a foraminifer dies without undergoing gametogenesis.

   The number of days until death was affected by the date of death ($p = 0.029$, Table 4) and the number of days after full / new moon ($p = 0.036$, Table 4).
   On the date of death of a foraminifer, using only data of foraminifera which did not undergo gametogenesis, significant explanatory factors were whether or not the foraminfer was caught during the lunar phase ($p = 0.028$, Table 5), the date on which the foraminifer was caught (linear regression, $p = 0.003$) and the Azores Current dependent grouping ($p = 0.001$, Table 5), including all group dependent explanatory variables (salinity ($p = 0.002$), temperature ($p < 0.001$), latitude ($p = 0.002$), longitude ($p = 0.003$), Table 4).

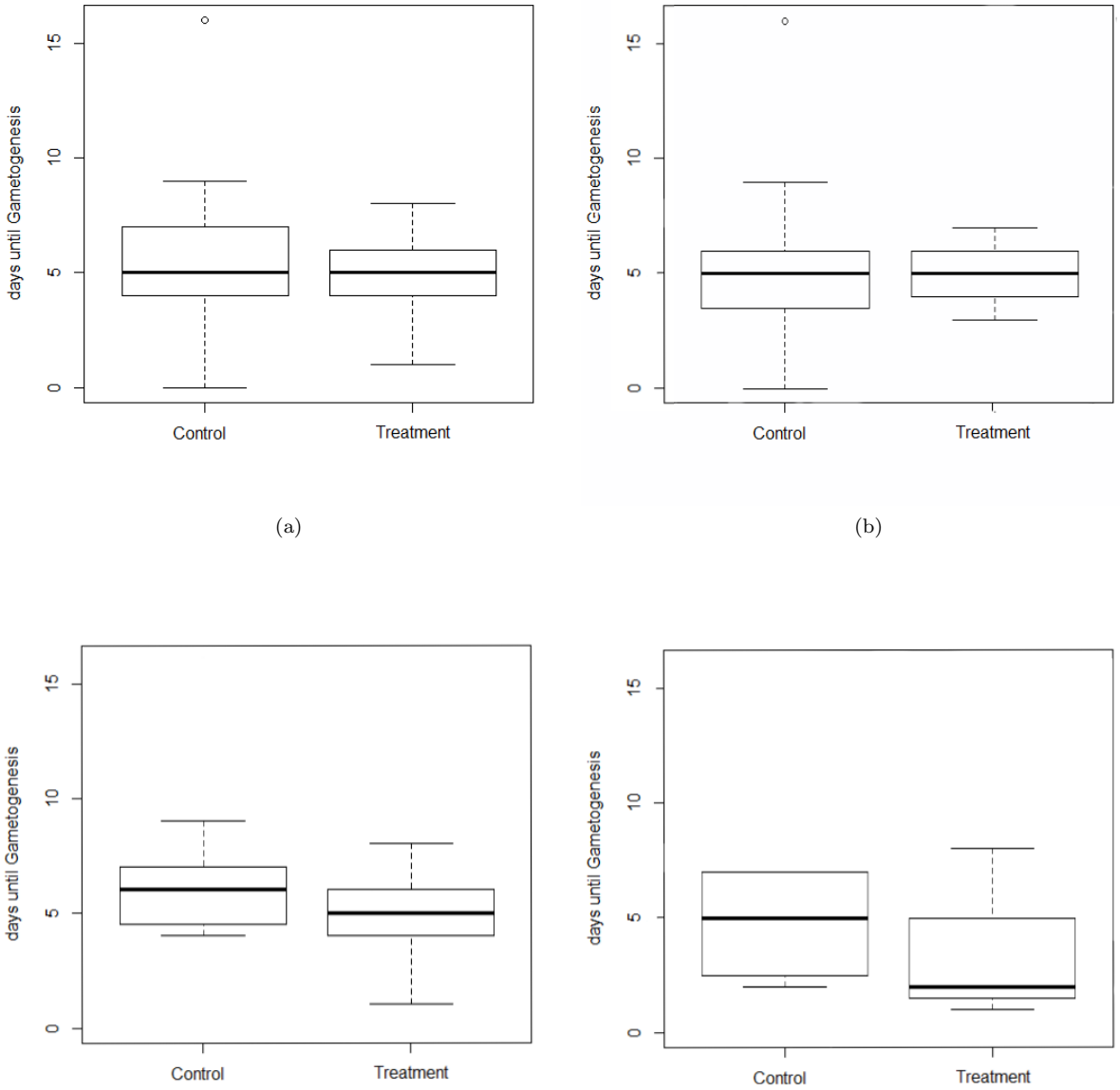


Figure 14: Number of days until foraminifera underwent gametogenesis for control and treatment, separated for the origin of foraminifera relative to the Azores Current (Fig. 6):
a) Foraminifera from all groups combined, b) Foraminifera caught north of the Azores Current, c) Foraminifera caught within the Azores Current, d) Foraminifera caught south of the Azores Current. The line shows the mean, boxes represent the interquartile range, whiskers show the maximum and minimum value and dots show outliers

5.4 Hypothesis 4

Treatment and control group differ from one another: the external magnetic field shows an effect on:

1. Whether or not a foraminifer undergoes gametogenesis.

   No significant difference between treatment and control on whether or not a foraminifer underwent gametogenesis was detected (p = 0.593, Table 3).

2. The number of days until gametogenesis.

   The number of days until gametogenesis was not significantly different between the control and the treatment (p = 0.396, Table 5, Fig. 14 a). This was confirmed using a mixed model with a random factor accounting for nesting of the data within the number of days until the end of the lunar phase at the time at which the foraminifer was set into the experiment (p = 0.397, Table 8). The boxplot showing the number of days until gametogenesis for the different groups however, show a tendency towards earlier gametogenesis within the treatment group for foraminifera sampled south of and within the Azores Current (Fig. 14 c, d)

3. The date on which foraminifera undergo gametogenesis.

   No significant effect of the experiment could be detected on the date on which foraminifera underwent gametogenesis (p = 0.388, Table 5). However, when assigning the mean, mode and median dates, it seems that foraminifera under treatment conditions underwent gametogenesis earlier than in the control group (also see Fig. 14 c and d).

Mean, mode and median of the dates, given as Julian day, on which the foraminifera in the control group and the treatment group underwent gametogenesis, for both the number and the ratio of foraminifera undergoing gametogenesis. nb = number

		Date (nb)	Lunar Phase (nb)	Date (ratio)	Lunar phase (ratio)
Control	Mean	272	No	272	No
	Mode	278	Yes	279	Yes
	Median	273	No	274	No
Treatment	Mean	270	No	271	No
	Mode	267	No	273	No
	Median	270	No	271	No

5.5 Hypothesis 5

Uncontrolled explanatory factors (e.g. colour variety of the foraminifer and the conditions a foraminifer was caught under) have an effect on:

1. The number of days until foraminifera undergo gametogenesis.

   Only the date on which the foraminifer underwent gametogenesis had a significant effect on the number of days until gametogenesis (p = 0.001, Table 4).

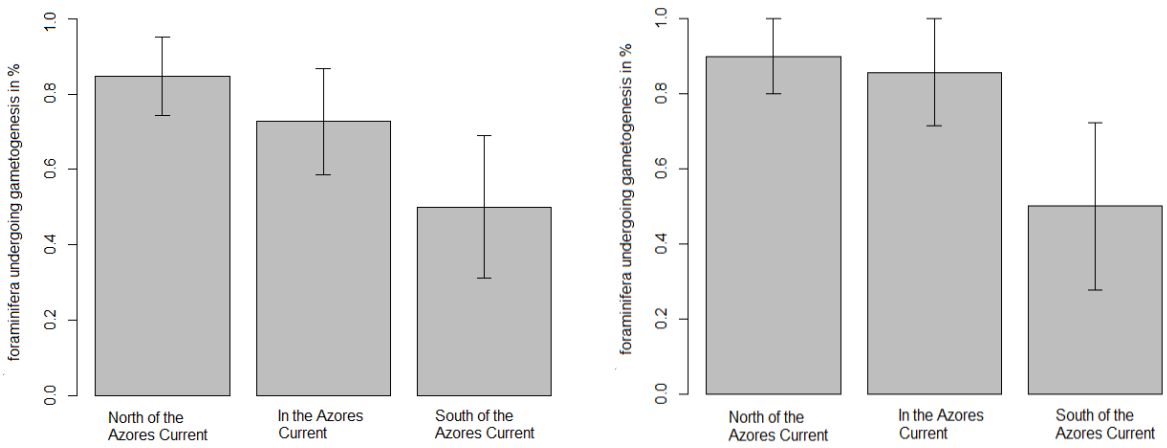


Figure 15: Group effect on the amount of foraminifera which underwent gametogenesis:
a) Control, b) Treatment. The mean ± SD is shown, grouping depends on the course of the Azores Current (Fig. 6).

2. Whether or not a foraminifer undergoes gametogenesis.

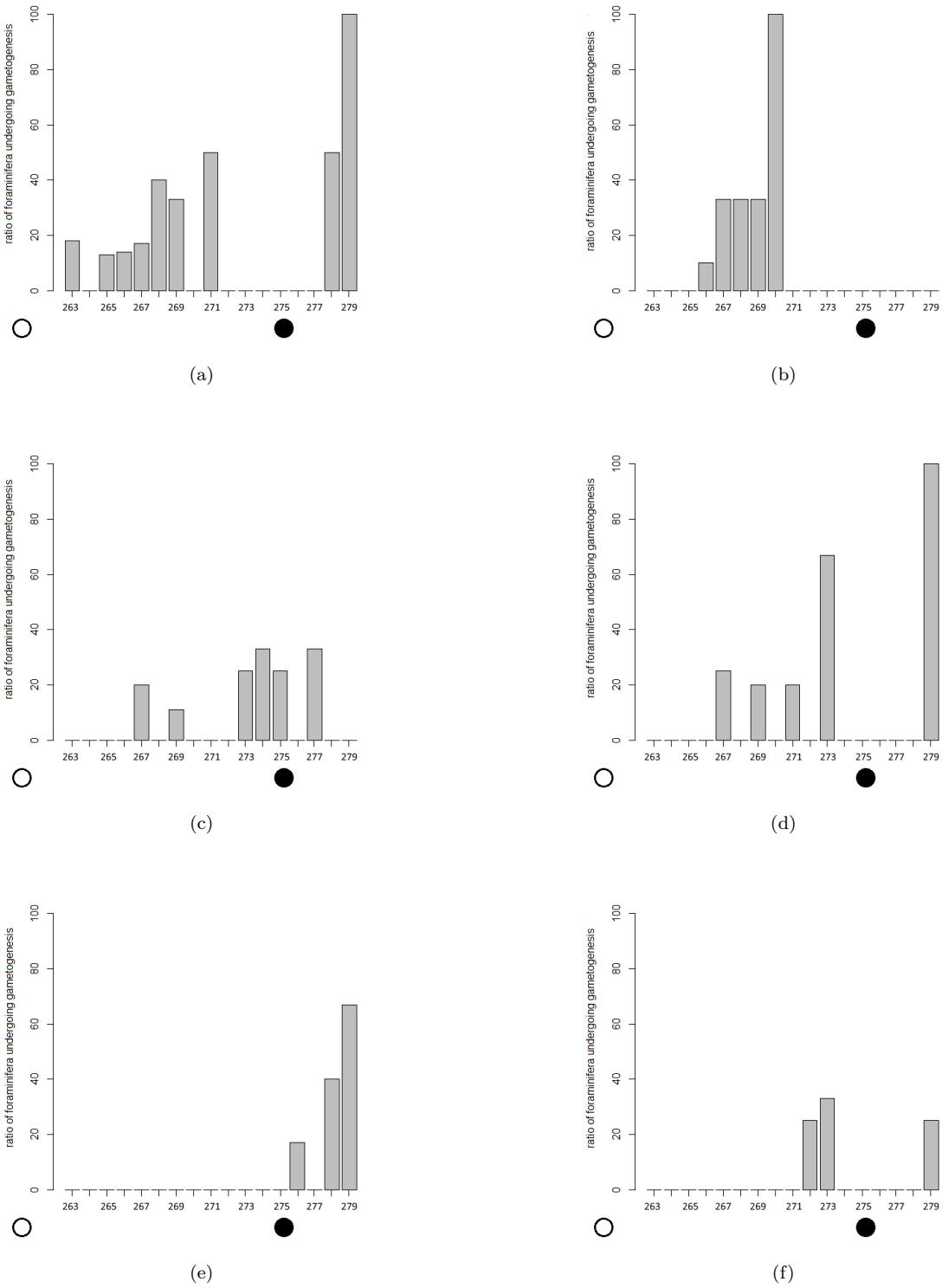
   When using logistic regression, the day on which a foraminifer was caught did have a significant effect on whether or not it underwent gametogenesis ($p = 0.033$, Table 3), as well as the Azores Current dependent grouping ($p = 0.021$, Table 3) and all group dependent explanatory variables (salinity: $p = 0.020$, temperature: $p = 0.046$, latitude: $p = 0.017$ and longitude: $p = 0.052$, Table 3). For foraminifera caught south of the Azores Current, the amount of foraminifera which underwent gametogenesis was lowest (Fig. 15).

3. The date on which foraminifera undergo gametogenesis.

   Whether or not a foraminifer was caught in the lunar phase ($p < 0.001$, Table 5), the days until the end of the lunar phase measured from the moment the foraminifer was set into the experiment ($p = 0.043$, Table 4), as well as the Azores Current dependent grouping ($p < 0.001$, Table 6) and all group dependent explanatory variables (salinity: $p < 0.001$, temperature: $p < 0.001$, latitude: $p < 0.001$ and longitude: $p < 0.001$, Table 4) showed a significant impact on the date of gametogenesis of foraminifera.

4. Whether or not gametogenesis of the foraminifer lies within the lunar phase.

   None of the uncontrolled explanatory factors had a significant impact on whether or not gametogenesis took place during the lunar phase when using a binary variable as an indicator for the lunar phase (Table 3, Figure 16).



(a) (b) (c) (d) (e) (f)

Figure 16: Comparison of the ratio of foraminifera undergoing gametogenesis over the time per Azores Current dependent grouping (Fig. 6) and experiment:
left: Control, right: Treatment, upper row: Foraminifera caught north of the Azores Current, middle: Foraminifera caught within the Azores Current, lower row: Foraminifera caught south of the Azores current.

5.6 Hypothesis 6

Interactions between controlled and uncontrolled explanatory variables have an effect on whether or not foraminifera undergo gametogenensis.

A mixed effects generalized linear model with a binomial error distribution and a log link function, allowing for interaction between the experiment and Azores Current dependent grouping, was used to test the influence of this interaction on whether or not foraminifera underwent gametogenesis, nested in the number of days until the end of the lunar phase at the time at which the foraminifer was set into the experiment. No variable was found to be significant (interaction: $p = 0.724$, group: $p = 0.104$, experiment: $p = 0.607$, Table 3). An interaction between the experiment and the date on which a foraminifer was caught also showed no significant influence (interaction: $p = 0.488$, date on which foraminifer was caught: $p = 0.124$, experiment:$p = 0.483$, Table 3).

5.7 Hypothesis 7

The floating behaviour is influenced by:

1. The experiment.

   No significant difference between treatment and control was found in the number of foraminifera floating ($p = 0.328$, Table 7). However, it has to be kept in mind that the sample size was extremely low, only 10 floating events were noted for 55 foraminifera over 17 days. In the treatment, 6 foraminifera were floating, whereas in the control 4 floating events were noted. For the control group, the lunar phase might have had an effect on the floating behaviour, as floating only occured during the lunar phase, whereas foraminifera in the treatment showed floating behaviour during the lunar and non-lunar phase. Due to the small sampling size, these numbers are not reliable.

2. The lunar phase.

   In total, floating was observed more often during the lunar phase (6 times versus 4 times), but, as before, the sampling size was too small to show significant differences ($p = 0.635$, Table 7) and for statistics to be reliable.

5.8 Hypothesis 8

Foraminifera for which floating behaviour is observed are more likely to undergo gametogenesis.

Due to the extremely low sampling size of reported floating behaviour, no statistical tests were performed. Only for 6 of the foraminifera reported to have been floating it could be determined whether or not they underwent gametogenesis: 4 did, whereas 2 did not. These numbers were equally distributed over control and treatment and are too low to be interpreted properly.

5.9 Summary

Hypothesis 1 was rejected for this experiment, as the observed effect of the lunar phase on the gametogenesis of foraminifera in the treatment group is thought to be caused by the treatment itself.

Hypothesis 2 is partially rejected: Foraminifera in the control group did not mainly undergo gametogenesis within the lunar phase, however, foraminifera in the treatment group mainly underwent gametogenesis outside the lunar phase.

Hypothesis 3.1 was accepted. The treatment did not have an observeable effect on the health of the foraminifera.

Hypothesis 3.2 was accepted, as all uncontrolled explanatory factors having an effect on the number of days until a foraminifer died or the date on which it died, are coupled to the date it was caught and thus are most likely an artefact of the sampling time than a meaningful effect.

Hypothesis 4.1 and 4.2 were accepted, the treatment did not observably influence the health of the foraminifera in the experiment.

Hypothesis 4.3 was not rejected: Even though no significant effect of the additional external magnetic field on the date on which foraminifera underwent gametogenesis was observed, a shift in the date on which they underwent gametogenesis was seen.

Hypothesis 5.1 was rejected, as only the day on which a foraminifer was caught influenced the number of days until it underwent gametogenesis, which is an artefact of the sampling time rather than a meaningful effect.

Hypothesis 5.2 was accepted, as the Azores Current dependent groups, were found to differ and all group dependent variables were found to have a significant influence on whether or not foraminifera underwent gametogenesis.

Hypothesis 5.3 was accepted, as the Azores Current dependent groups of foraminifera used in the experiment showed significant differences for the date of gametogenesis.

Hypothesis 5.4 was rejected, none of the uncontrolled explanatory variables had an influence on whether or not the date on which foraminifera underwent gametogenesis lay within the lunar phase.

Hypothesis 6 was rejected, no interactions of explanatory variables were found for whether or not foraminifera underwent gametogenesis.

Hypothesis 7 and 8 can not be judged based on the results of this experiment, as the amount of floating foraminifera was too low to predict influences of the lunar phase and the additional magnetic field on the floating behaviour or detect differences in the gametogenesis behaviour of foraminifera based on whether or not they have been reported as floating.

6 Discussion

6.1 Interpretations of the results

The effect of an external magnetic field on the planktonic foraminifer *G. ruber* was tested to investigate whether or not the lunar induced changes of the Earth's magnetic field could act as a trigger for simultaneous gametogenesis, which was hypothesized by Bijma et al (1990). Different hypotheses were tested in order to get an idea of the effects of an external magnetic field on the gametogenesis of *G. ruber*. Some evidence was found that an external magnetic field can trigger gametogenesis in *G. ruber*. However, one has to keep in mind that the magnetic field strength used in this experiment was much larger than the lunary induced fieldchanges of the Earth's magnetic field (69 μT versus 10 - 100 nT). More experiments testing the effect of a more natural magnetic field change need to be conducted.

***G. ruber* undergoes gametogenesis within the lunar phase**
(here defined as the day of full/ new moon + 4 days, see Hypothesis 1, 2 and 4 a)

The hypothesis that *G. ruber* in natural conditions undergoes gametogenesis within the lunar phase (Bijma et al., 1990a) could not be tested with this experiment. In the control group, no significant influence of the lunar phase on whether or not foraminifera underwent gametogenesis was found (Table 4). However, the mode of the dates on which foraminifera in the control group underwent gametogenesis lay within the lunar phase (see results of Hypothesis 4.3). Moreover, figure 12 a and 13 show that within the lunar phase there was a slightly higher percentage for the ratio of foraminifera (Equation 1) which underwent gametogenesis (52%). This might be explained by an additional internal zeitgeber, which can be overwritten by the external trigger of a changing magnetic field strength.
However, foraminifera also underwent gametogenesis outside of the lunar phase (ratio: 48%). That the percentage of foraminifera in the control group which underwent gametogenesis within the lunar phase is only 4% higher might show that the external lunar trigger was not detectable aboard the ship. The gametogenesis events in the control group were distributed nearly equally over the time of the experiment.
As the culturing took place aboard a ship, the metal shielded the foraminifera from the Earth's magnetic field and also from the lunary incuced magnetic field changes (Moore Jr, 1992). On board, a magnetic field with a strength of 45 μT $\pm$15 (SD)(mean drift of the magnetometer over the measuring time = 8 μT), which is similar to the mean Earth's magnetic field strength (50 μT), was measured. No significant interaction between the date and this magnetic field strength was detectable (Table 4). As the ship was predominantly going from north to south (Fig. 7), this can be seen as a confirmation that the magnetic field aboard was created by electronic devices, otherwise the magnetic field strength would have changed over time (Fig. 2). So, foraminifera in the control group experienced a magnetic field strength of roughly the same size as they already did in the ocean (Fig. 2), only without the change of the magnetic field strength at full / new moon, i.e. the proposed trigger for gametogenesis (Bijma et al., 1990a), and without the field strength changes across the globe.

As foraminifera of the control group were treated the exact same way as foraminifera in the treatment, except for the additional external magnetic field, the lack of a clear peak of gametogenesis events within the lunar phase can be seen as an indication that the changes of the Earth's magnetic field might indeed be the trigger for the synchronization of the gamete release of *G. ruber* and supports the hypothesis by Bijma et al. (1990).
The daily fluctuations of the ship's magnetic field in the order of $\sim$15 μT might have acted as a trigger for gametogenesis, causing the foraminifera to undergo gametogenesis over the whole time of the experiment without an observeable pattern.
The lunar phase had no influence on the health of a foraminifer, as no effect of the lunar phase on the amount of foraminifera that died was found.

Foraminifera in an external magnetic field show a trend towards earlier gametogenesis (see Hypothesis 2 and 4.3)

The treatment had no significant effect on the number of days until a foraminifer underwent gametogenesis (Table 4). However, when looking at figures 13 and 14 c and d, one can see that foraminifera in the treatment group seem to undergo gametogenesis a bit earlier than foraminifera in the control group. This is also seen in the mean, mode and median of the dates on which foraminifera underwent gametogenesis (see results of H 4.1).
One reason for the earlier gametogenesis might be, that the gamete release was caused by stress, a phenomenon that has been reported e.g. for *Holothuria fuscogilva* (Ramofafia et al., 2000). The stressor would then be the magnetic field, as there was no other difference between foraminifera in the control group and the ones in the treatment group, thus foraminifera would react on the external magnetic field.
Most of the foraminifera in the treatment group underwent gametogenesis outside of the lunar phase (Fig. 12 b, d, 13). I hypothesize that the reason for this is a shift in the time when foraminifera undergo gametogenesis. I propose that this shift is caused by the external magnetic field that was applied to them.
In total, the mean number of days until foraminifera underwent gametogenesis was similar for treatment (4.7 $\pm$ 2.1 (SD)) and control (5.5 $\pm$ 3.2 (SD)), however, the standard deviation for the control group is larger, which can be taken as a hint that the simultaneousness of the foraminifera in the control group is less precise than the one for the treatment group. This supports the idea that foraminifera have an internal zeitgeber (Spindler et al., 1979) and react on an external trigger which synchronizes gametogenesis and overwrites the internal zeitgeber (Bijma et al., 1990a).
The shift in the gametogenesis of *G. ruber* in the treatment group supports the hypothesis by Bijma et al (1990) that the semilunarity of the gametogenesis in *G. ruber* is not caused by an internal zeitgeber but that the tidally induced changes of the Earth's magnetic field act as a trigger for this simultaneous gametogenesis. But how can foraminifera detect changes of the Earth's magnetic field?
In 2011, a magnetite bearing foraminifer was described by Pawlowski and Majewski. Even though the described species (*Psammophaga magnetica*) is benthic, bearing magnetite and other magnetic metals might be the mechanism behind a sensitivity towards magnetic field changes. So far, such metals have not been discovered for planktonic foraminifera. However, all planktonic foraminifera contain fibrillar bodies, which are supposed to be floating devices (Hemleben et al., 2012). I propose that these fibrillar bodies might contain the needed magnetogenic material and thus act as a

sensory organelle to detect the differences in the Earth's magnetic field which are caused by the lunar phases. The idea is that the magnetic field change needs to exceed a certain threshold for the foraminifer to undergo gametogenesis, otherwise they might get triggered with each tide (i. e. every day), which is conform with the hypotheses by Bijma et al (1990).
There are also some benthic foraminifera which are supposed to be geotactic, i.e. they orient themselves using gravity (Duijnstee et al., 2003), which generally decreases with the altitude (Newton, 1687). However, the Earth's magnetic field also has a vertical component (Haak et al., 2003). Thus, the observed geotaxis might in truth be magnetotaxis. However, the lunar cycle does not only affect the Earth's magnetic field but mainly influences the gravity on earth (Newton, 1687). Due to the experiments conducted for this thesis I propose that the change in the Earth's magnetic field strength is more likely the trigger for gametogenesis in *G. ruber* than the gravitational changes, though future research is needed to clarify this.

The number of days until death did not differ between treatment and control, so no lethal effect of the magnetic field could be detected (Table 5). No significant effect of the experiment was detected on whether or not foraminifera underwent gametogensis (Table 3). This can be interpreted as a sign of health of the used foraminifera: the experiment did not influence whether foraminifera underwent gametogenesis, thus all foraminifera were healthy enough to be able to undergo gametogenesis.

The Azores Current might serve as a barrier for cryptic speciation (see Hypothesis 3 and 4)

A difference in the amount of formainifera undergoing gametogenesis was detected for the Azores Current dependent groups (Fig. 15). It could be argued that the likeliness for foraminifera to undergo gametogenesis, and thus the number of foraminifera which underwent gametogenesis, was lower for foraminifera caught south of the Azores Current, as they were the ones that were caught and exposed to experimental conditions latest (Table 1, 2 and Fig. 6). However, no significant linear regression could be fitted between the number of foraminifera which underwent gametogenesis and the time they spent in the experiment, thus this explanation cannot be held (Table 4). The difference between the groups could be due to a cryptic speciation with the Azores Current serving as a barrier (de Vargas et al., 1999).
The group-dependent differences on the date of gametogenesis, however, might be an artefact of the difference in the date on which the foraminifera were caught. The number of days until gametogenesis does not differ much between the control groups (Fig. 14). Foraminifera in the control group stemming from south of the Azores Current take as long for gametogenesis as foraminifera stemming from north or within the current. For foraminifera under treatment, gametogenesis occured fastest for foraminifera caught south of the Azores Current (Fig. 14). This could imply that foraminifera from southern regions react stronger on the magnetic trigger, especially as no significant difference of the Azores Current dependent grouping on whether or not foraminifera underwent gametogenesis within the lunar phase was found (Table 3). As the Earth's magnetic field is weaker further towards the equator (Fig. 2), the lunary induced changes should make up for a greater fraction of the experienced magnetic field as such, thus foraminifera near the equator might react stronger on this external trigger than foraminifera further north. One has to keep in mind though, that foraminifera from south of the Azores Current were the ones that entered the

experiment latest. Thus, the longest period in which they stayed in the experiment was 8 days, before the experiments had to be stopped, which leads to a bias in judging the duration until gametogenesis. However, the effect of the group-dependent factors are much stronger parameters than the date on which the foraminifer was caught (Table 4). This can be seen as an indication that not only the date of catching the foraminifer had an impact on the date of gametogenesis, but also that between the groups there was a significant difference mainly caused by the salinity and temperature differences of where the foraminifer was caught. One reason for the different behaviour of the groups could be that the Azores Current serves as a barrier for foraminifera, that cryptic speciation took place due to this barrier (de Vargas et al., 1999) and that there is a genetic difference between foraminifera caught north and south of the current. Another reason might be, that foraminifera from further south are adapted to higher temperatures than the ones in the north.

As the temperature in the culturing room was 20°C, this could have caused the foraminifera from further south to undergo gametogenesis later, due to a slower metabolism in the colder temperatures (van't Hoff rule, e.g. Gillooly et al., 2001). Foraminifera from further north are less affected by this, as the water they are adapted to is colder, thus the change of temperature is smaller for them than for the foraminifera from stations further south.

The same factors also influenced the date of death of foraminifera. Foraminifera from further south might have died later because their metabolism is slowed down more than that of the foraminifera stemming from north of the current or because they have a different life span.

That none of the uncontrolled factors had a significant influence on whether or not gametogenesis took place within the lunar phase can be interpreted in such a way that any effects observed between lunar phase and non-lunar phase are induced by either the lunar phase itself (full or new moon) or the experiment (treatment or control). As no lunary influenced changes of the Earth's magnetic field could be measured (Table 4), and only the treatment group showed an effect on the lunar phase, I propose that no effect of the lunar phase itself was detected but only an effect of the experiment.

The absence of a significant interaction between both the Azores Current dependent grouping interacting with the experiment and the day on which a foraminifer was caught interacting with experiment, both nested within the number of days until end of the lunar phase at insertion of the foraminifer into the experiment, supports the idea that no effect of the lunar phase was observed but only an effect of the experiment. However, there were many missing values, as the sampling size was too low and the experimental design was unbalanced (Table 1, 2), so that data was not available for all combinations, which biasses the results.

Proposed correlation between floating behaviour and gametogenesis rate

The number of floating foraminifera was too low for meaningful statistical analysis (10 floating events for 55 foraminifera over 17 days). However, more foraminifera were detected floating during the lunar phase compared to the non-lunar phase and in the treatment group compared to the control group (6 versus 4 for both). This might be an indicator that the floating behaviour correlates with gametogenesis, as foraminifera which undergo gametogenesis usually move to different water layers, i.e. their buoyancy changes. If the fibrillar bodies contain magnetic materials and if they are floating devices, changes of the Earth's magnetic field might induce a reaction in the fibrillar bodies, resulting in gametogenesis to happen and in an adjustment of buoyancy.

More foraminifera that were observed to be floating one day underwent gametogenesis than died (4 versus 2). The sampling size is too low for proper interpretation, however this might be a hint that floating behaviour and gametogenesis are connected.

Gametogenesis is influenced by lunary induced changes in the Earth's magnetic field

During this study, it was detected that *G. ruber* in an environment with a relatively stable magnetic field does not undergo gametogenesis as simultaneously as it is proposed to do in the ocean (Bijma et al., 1990a). This can be seen as an indicator that changes in the Earth's magnetic field act as a trigger for foraminiferal gametogenesis. When *G. ruber* was introduced to an additional magnetic field, a more simultaneous gametogenesis pattern was observed. Thus, the additional external magnetic field might have acted as a trigger for simultaneous gametogenesis. Such an external trigger can influence a possible internal zeitgeber's oscilliation for gametogenesis (Rensing, 1973), resulting in the semiluar periodicity of gametogenesis. Approximately 5 days after experiencing the trigger, foraminifera underwent gametogenesis. In the control without a trigger, gametogenesis took place one day later. Even though these differences were not statistically significant, this could be a sign that an internal zeitgeber exists, however it is less precise than the external trigger and is under natural conditions overwritten by the external trigger. The observed reactions on a magnetic field strongly support the idea that the gametogenesis in *G. ruber* is induced by changes of the Earth's magnetic field (Bijma et al., 1990a).

6.2 Future research

The results of the conducted experiments need to be supported by further studies. The next step will be to repeat the experiments with a larger sampling size and during a longer time period on land. Being on land excludes possible effects from the change of the Earth's magnetic field across the globe. Additionally, one could create an area that is nearly free of magnetic fields by using special magnetic field shields which can insulate up to 90% of the magnetic field strength. Using them would make it possible to see whether or not foraminifera in a magnetic field free environment will still undergo gametogenesis, and if yes, when they will do it. The results of the experiments conducted for this thesis imply that foraminifera under such a treatment would still undergo gametogenesis, however not mainly within the lunar phase and not simultaneously. As a control, one could on the one hand do net hauls directly in the area where the experimental specimen come from to gain information about their natural gametogenesis behaviour, and, on the other hand, have an untreated group which is not shielded from the Earth's magnetic field.
Another treatment would be a setup, where foraminifera are shielded from all external magnetic fields but with an internal artificial magnetic field which has the same field strength of the area where they originate from. For this group one could induce changes of the magnetic field strength and thus might trigger gametogenesis events.
Most importantly, the change of the magnetic field strength needs to be adapted to the real changes of the Earth's magnetic field during the lunar phase.
Another important experiment will be to examine if foraminifera possess an organelle that is able to detect the changes in the field strength of the Earth's magnetic field, and how it works. The fibrillar bodies seem to be a promising start and might be a combination of floating and magnetic field strentgh sensing organelle. An experiment testing whether foraminifera (benthic or plank-

tonic) are attracted or repelled by a magnetic field might help finding out more. If foraminifera show a clear magnetotactic behaviour, this would be strong evidence for them being capable of reacting to changes in the strength of the Earth's magnetic field.
The genetic examination of foraminifera from different areas across the major oceanic current systems would be interesting in terms of finding possible genetic explanations for the here observed different behaviours of the foraminifera caught north, south and within the Azores Current. Genetic examination would help to identify whether the cause of this different behaviour is due to different haplotypes, different adaptations or the formation of subpopulation, subspecies or even cryptic species.
It would also be interesting to see, whether other foraminifera (e.g. *Orbulina universa*) and planktonic organisms react on changes of the strength of the Earth's magnetic field

7 Conclusions

The experiments conducted within this MSc project show, that field strength changes by using an additional external magnetic field might serve as a trigger for gametogenesis in the planktonic foraminifer *G. ruber*. This strongly supports the idea of the external trigger for simultaneous gametogenesis in *G. ruber* being lunary induced changes of the Earth's magnetic field strength (Bijma et al., 1990a). Furthermore, foraminifera caught north, within and south of the Azores Current, showed significant differences for the amount of foraminifera which underwent gametogenesis and for the duration until gametogenesis and death of foraminifera, as well as for the date of death and / or gametogenesis. This might be a hint that the Azores Current acts as a barrier, causing cryptic speciation of *G. ruber*. This experiment is the first one to test the effect of an external magnetic field on the gametogenesis of *G. ruber* and most likely the first one to do so for planktonic organisms in general.

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8 Appendix

All statistical results are seperated for the test that was used. The table for logistic regression also contains the results of the nested mixed effects generalized linear models with a binomial error distribution and a log link function allowing for interactions.
Foraminifera were caught in the Azores Current region and cultured aboard the RV *Maria S. Merian* during the MSM58 cruise. An experiment was conducted testing for the effect of an additional external magnetic field on the gametogenesis of *Globigerinoides ruber*. Foraminifera of the treatment group were exposed to an additional magnetic field of the strength of ~ 69 μT.

Table 1: Raw data control
Dates are given as Julian day. Latitude and longitude are given in degrees decimal. C = Control group

ID	Gametogenesis	Start date	Death date	Catch date	Station	Colour variety	Salinity	Temperature	Latitude	Longitude
C1(neu)	Yes	264	269	261	12	White	36	21	40.88	-30.88
C2	No	262	264	261	10	White	36	21	40.72	-29.93
C2(neu)	No	265	279	264	16	White	36.4	23.7	37.56	-33.13
C3	Yes	262	265	261	10	White	36	21	40.72	-29.93
C3.1	Yes	268	275	267	28	White	36.3	23.7	38.58	-35.54
C4	Yes	262	263	261	10	White	36	21	40.72	-29.93
C5	No	262	264	261	10	White	36	21	40.72	-29.93
C5.1	Yes	265	269	264	16	White	36.4	23.7	37.56	-33.13
C6.1	Yes	263	267	267	28	White	36.3	23.7	38.58	-35.54
C7	Yes	262	278	261	10	White	36	21	40.72	-29.93
C8.1	Yes	268	274	267	28	White	36.3	23.7	38.58	-35.54
C9.2	Yes	262	268	262	12	White	36	22	40.88	-30.88
C9.4	Yes	275	279	262	12	White	36	22	40.88	-30.88
C9(1)	Yes	263	263	262	12	White	36	22	40.88	-30.88
C10	Yes	262	266	261	10	White	36	21	40.72	-29.93
C11.1	No	271	272	270	34	White	36.5	24.5	35.65	-35.5
C12.1	Yes	268	273	266	24	White	36.4	23.7	37.86	-34.18
C13	Yes	262	271	261	10	White	36	21	40.72	-29.93
C13.1	No	274	274	273	43	White	36.7	25	33.91	-38.66
C14.1	Yes	268	277	268	28	White	36.3	23.7	38.58	-35.54
C15	Yes	262	267	261	10	White	36	21	40.72	-29.93
C15.1	No	268	278	267	28	White	36.3	23.7	38.58	-35.54
C16	Yes	262	268	261	10	White	36	21	40.72	-29.93
C16.1	Yes	271	278	270	34	White	36.5	24.5	35.65	-35.5
C17.2	No	274	279	272	40	White	36.7	25	33.95	-36.25
C18	No	266	267	266	23	White	36.4	23.7	37.61	-34.38
C18.1	Yes	268	274	266	24	White	36.4	23.7	37.86	-34.18
C19.1	No	274	279	270	34	White	36.5	24.5	35.65	-35.5
C20	Yes	266	273	265	20	White	36.4	23.7	37.74	-33.94
C20.1	Yes	274	276	271	38	White	36.5	24.5	35.29	-35.79
C22.2	Yes	275	278	274	47	White	36.9	25.5	32.33	-39.66
C23	Yes	272	279	271	38	Pink	36.5	24.5	35.29	-35.79

Table 2: Raw data treatment
Dates are given as Julian day. Latitude and longitude are given in degrees decimal. MB = Treatment group: Foraminifera were exposed to an external magnetic field of the strength of 69 μT.

ID	Gametogenesis	Start date	Death date	Catch date	Station	Colour variety	Salinity	Temperature	Latitude	Longitude
MB1.2	No	274	279	272	40	White	36.7	25	33.95	-36.25
MB2	Yes	263	266	262	12	White	36	22	40.88	-30.88
MB4	Yes	263	267	262	12	White	36	22	40.88	-30.88
MB5	Yes	263	269	262	12	White	36	22	40.88	-30.88
MB5.1	No	271	279	270	34	White	36.5	24.5	35.65	-35.5
MB6.1	Yes	265	269	264	16	Pink	36.4	23.7	37.56	-33.13
MB7	Yes	263	270	262	12	White	36	22	40.88	-30.88
MB8.1	Yes	268	273	267	28	White	36.3	23.7	38.58	-35.54
MB9	Yes	263	267	262	12	White	36	22	40.88	-30.88
MB9.1	Yes	268	273	267	28	White	36.3	23.7	38.58	-35.54
MB10.1	Yes	265	271	264	16	White	36.4	23.7	37.56	-33.13
MB11.2	No	274	279	273	43	White	36.7	25	33.91	-38.66
MB12	Yes	263	268	262	12	White	36	22	40.88	-30.88
MB12.1	Yes	271	279	269	31	White	36.5	24	35.01	-33.68
MB13	Yes	263	267	262	12	White	36	22	40.88	-30.88
MB14.1	Yes	271	279	270	33	White	36.5	24.5	35.66	-35.53
MB15	Yes	263	268	262	12	White	36	22	40.88	-30.88
MB15.1	Yes	271	272	270	34	White	36.5	24.5	35.65	-35.5
MB16	No	263	268	262	12	White	36	22	40.88	-30.88
MB16.1	No	265	271	264	16	White	36.4	23.7	37.56	-33.13
MB17	Yes	263	270	262	12	White	36	22	40.88	-30.88
MB17.1	Yes	271	273	270	34	Pink	36.5	24.5	35.65	-35.5
MB20	Yes	266	267	266	23	White	36.4	23.7	37.61	-34.38

Table 3: Statistical data Logistic Regressions: P (y = 1) = the estimated probability that the response variable (y) is positive (Yes), only significant equations are given. DF = Degrees of freedom, N = Sampling size, p = Porbability value.
y (Response variables): 2 = Whether or not a foraminifer underwent gametogenesis, 5 = Whether or not gametogenesis of foraminifera took place during the lunar phase
x (Explanatory variables): 1 = Experiment, 2 = Lunar indicator for the day of gametogenesis: b = Days after full/ new moon, c = Days until the end of the lunar phase, starting on the day on which foraminifera were put into the experiment, 3 = Colour variety of the foraminifer (pink or white), 4 = Azores Current dependent grouping: a = Salinity, b = Temperature, c = Latitude, d = Longitude, 5 = Days until death of the foraminifer, 7 = Date on which the foraminifer was caught, 8 = Whether or not the foraminifer was caught during the lunar phase

y	x	DF	N total	log ratio	Equation (P (y = 1) =)	p
2	1	1	55	0.291		0.590
	2 b	1	55	3.052		0.081
	2 c	1	55	0.674		0.412
	4	1	55	5.918	$\frac{1}{1+e^{(2.9924+(-0.9671)*x)}}$	**0.015**
	4 a	1	55	63	$\frac{1}{1+e^{(118.446+(-3.232)*x)}}$	**0.012**
	4 b	1	55	4.647	$\frac{1}{1+e^{(13.3645+(-0.5272)*x)}}$	**0.031**
	4 c	1	55	6.384	$\frac{1}{1+e^{(-11.0606+0.3203*x)}}$	**0.012**
	4 d	1	55	4.126	$\frac{1}{1+e^{(9.2969+0.2441*x)}}$	**0.042**
	5	1	55	2.21e-010		0.815
	7	1	55	4.860	$\frac{1}{1+e^{(46.85695+(-0.17206)*x)}}$	**0.027**
	8	1	55	1.752		0.186
5	1	1	41	5.380	$\frac{1}{1+e^{(-0.6466+(-1.7047)*x)}}$	**0.020**
	2 c	1	41	1.205		0.272
	3	1	41	0.153		0.695
	4	1	41	0.700		0.403
	4 a	1	41	0.394		0.530
	4 b	1	41	0.209		0.648
	4 c	1	41	1.039		0.308
	4 d	1	41	0.502		0.479
	7	1	41	1.603		0.206
	8	1	41	1.062		0.303
2	1 * 4 nested in 2 c	0	0.880	NA		0.724
	1 nested in 2 c	0	2.031	NA		0.607
	4 nested in 2 c	0	0.527	NA		0.104
2	1*7 nested in 2 c	0	0.162	NA		0.488
	1 nested in 2 c	0	43.176	NA		0.483
	7 nested in 2 c	0	0.088	NA		0.124

Table 4: Statistical data Linear Regressions: only significant equations are given. DF = Degrees of freedom, F = F-ratio, N = Sampling size, R^2 = Coefficient of determination, p = Probability value.
y (Response variables): 1 = The number of foraminifera which underwent gametogenesis per day: a = Ratio of foraminifera which underwent gametogenesis in control, b = Number of foraminifera which underwent gametogenesis in control, c = Ratio of foraminifera which underwent gametogenesis in treatment, d = Number of foraminifera which underwent gametogenesis in treatment, 3 = The date on which foraminifera underwent gametogenesis, 4 = The date on which a foraminifer died, 6 = The days it took until a foraminifer underwent gametogenesis, starting on the day on which the foraminifer was put into the experiment, 7 = The days it took until a foraminifer died, starting on the day on which the foraminifer was put into the experiment, 9 = The number of foraminifera undergoing gametogenesis after a certain amount of days, MFS = Magnetic field strength
x (Explanatory variables): 2 = Lunar indicator for the day of gametogenesis: b = Days after full / new moon, c = Days until the end of the lunar phase, starting on the day on which foraminifera were put into the experiment, 4 = Azores Current dependent grouping: a = Salinity, b = Temperature, c = Latitude, d = Longitude, 6 = Date on which foraminifera underwent gametogenesis, 7 = Date on which the foraminifer was caught, 10 = Days until gametogenesis

y	x	DF	F	N total	R^2	Equation (y =)	p
1 a	2 b	1	0.405	32	0.026		0.534
1 b	2 b	1	0.010	100	0.001		0.923
1 c	2 b	1	5.470	23	0.267	0.4237 + 2.2303 * x	**0.034**
1 d	2 b	1	3.895	100	0.206	0.1994 + 0.1305 * x	**0.067**
3	2 b	1	1.936	41	0.048		0.172
	2 c	1	4.400	41	0.101	269.4222 + 0.3025 * x	**0.043**
	4 a	1	24.880	41	0.390	-176.87 + 12.37 * x	**<0.001**
	4 b	1	24.010	41	0.381	221.1661 + 2.189 * x	**<0.001**
	4 c	1	28.630	41	0.423	322.738 + (-1.3279) * x	**<0.001**
	4 d	1	25.000	41	0.391	232.8624 + (-1.1658) * x	**<0.001**
	7	1	35.630	41	0.477	36.8784 + 0.8849 * x	**<0.001**
4	2 b	1	0.400	14	0.032		0.539
	2 c	1	0.812	14	0.063		0.385
	4 a	1	16.630	14	0.581	-363.832 + 17.508 * x	**0.002**
	4 b	1	24.730	14	0.673	191.7471 + 3.4533 * x	**<0.001**
	4 c	1	15.140	14	0.558	336.4592 + (-1.7014) * x	**0.002**
	4 d	1	14.450	14	0.546	219.7484 + (-1.5635) * x	**0.003**
	7	1	14.410	14	0.546	10.8175 + 0.9828 * x	**0.003**
6	2 b	1	0.369	41	0.010		0.842
	2 c	1	0.040	41	0.001		0.842
	4 a	1	0.252	41	0.006		0.619
	4 b	1	0.449	41	0.011		0.507
	4 c	1	0.231	41	0.006		0.633
	4 d	1	0.252	41	0.006		0.618
	6	1	14.400	41	0.270	-78.49101 + 0.30843 * x	**0.001**
	7	1	0.178	41	0.005		0.676
7	2 b	1	5.539	14	0.316	8.2286 + (-0.6) * x	**0.036**
	2 c	1	3.460	14	0.224		0.088
	4 a	1	0.007	14	0.001		0.934
	4 b	1	0.195	14	0.016		0.667
	4 c	1	0.021	14	0.002		0.888
	4 d	1	0.003	14	0.000		0.954
	6	1	6.115	14	0.338	-97.2074 + 0.3731 * x	**0.029**
	7	1	0.123	14	0.010		0.732
9	10	1	0.189	41	0.021		0.674
MFS	Date	1	1.736	67	0.026		0.192

Table 5: Statistical data ANOVAs: DF = Degrees of freedom, F = F-ratio, N = Sampling size, p = Probability value.
y (Response variables): 1 = The number of foraminifera which underwent gametogenesis per day: a = Ratio of foraminifera which underwent gametogenesis in control, b = Number of foraminifera which underwent gametogenesis in control, d = Number of foraminifera which underwent gametogenesis in treatment, , 3 = The date on which foraminifera undergo gametogenesis, 4 = The date on which a foraminifer died, 6 = The days it took until a foraminifer underwent gametogenesis, starting on the day on which the foraminifer was put into the experiment, 7 = The days it took until a foraminifer died, starting on the day on which the foraminifer was put into the experiment
x (Explanatory variables): 1 = Experiment, 2 = Lunar indicator for the day of gametogenesis: a = Binary variable (does the day lie within the lunar phase), 3 = Colour variety of the foraminifer (pink or white), 4 = Azores Current dependent grouping, 7 = Date on which the foraminifer was caught, 8 = Whether or not the foraminifer was caught during the lunar phase

y	x	DF	F	N total	comments	p
1 a	2 a	1	1.322	100		0.268
1 b	2 a	1	5.984	32	non-homogeneous variances but sufficiently normally distributed	**0.027**
1 d	2 a	1	0.086	23		0.773
3	1	1	0.763	41		0.388
	8	1	24.932	41	non-homogeneous variances but sufficiently normally distributed	<**0.001**
4	4	1	19.032	14	Group 1 different from others	**0.001**
	8	1	6.249	14		**0.028**
6	1	1	0.737	41	sufficiently normally distributed	0.396
	2 a (yes)	1	0.948	41	non-homogeneous variances but sufficiently normally distributed	0.336
	2 a (no)	1	0.948	41	non-homogeneous variances but sufficiently normally distributed	0.336
	3	1	0.270	41	sufficiently normally distributed	0.606
	4	1	0.278	41	sufficiently normally distributed	0.601
	7	1	0.002	41	sufficiently normally distributed	0.968
7	1	1	0.383	14	sufficiently normally distributed	0.548
	4	1	6.00e-004	14		0.981
	8	1	0.383	14		0.548

Table 6: Statistical data Kruskal-Wallis-Test: DF = Degrees of freedom, N = Sampling size, Chi^2 = Chi-squared test statistic, p = Probability value.
y (Response variables): 1 c = Ratio of foraminifera which underwent gametogenesis in treatment , 3 = The date on which foraminifera underwent gametogenesis, 4 = The date on which a foraminifer died
x (Explanatory variables): 1 = Experiment, 2 = Lunar indicator for the day of gametogenesis: a = Binary variable (does the day lie within the lunar phase), b = Days after full / new moon, c = Days until the end of the lunar phase, starting on the day on which foraminifera were put into the experiment, 3 = Colour variety of the foraminifer (pink or white), 4 = Azores Current dependent grouping

y	x	DF	N total	Kruskal Chi^2	comments	p
1 c	2 a	8	100	8.229		0.412
3	3	1	41	1.114		0.291
	4	2	41	16.475	all groups different from one another	**<0.001**
4	1	1	14	1.686		0.194

Table 7: Statistical data Fisher's exact test: N = sampling size, p = Probability value.
y (Response variables): 2 = Whether or not a foraminifer underwent gametogenesis, 8 = The floating behaviour of foraminifera
explanatory variables (x): 1 = Experiment, 2 = Lunar indicator for the day of gametogenesis: a = Binary variable (does the day lie within the lunar phase), 3 = Colour variety of the foraminifer (pink or white)

y	x	odds ratio	N total	p
2	3	0.138	55	0.562
8	1	0.092	309	0.328
	2 a	0.635	309	0.177

Table 8: Statistical data ANCOVA: DF = Degrees of freedom, F = F-ratio, N = Sampling size, p = Probability value.
y (Response variables): 6 = The days it took until a foraminifer underwent gametogenesis, starting on the day on which the foraminifer was put into the experiment
x (Explanatory variables): 1 = Experiment, 2 = Lunar indicator for the day of gametogenesis: c = Days until the end of the lunar phase, starting on the day on which foraminifera were put into the experiment

y	x	DF	F	N total	p
6	1 nested in 2 c	1	0.737	41	0.397

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I hereby declare that the thesis submitted is my own unaided work. All direct or indirect sources used are acknowledged as references. The written thesis corresponds with the thesis in its digital form. I further declare that this thesis was not previously presented to another examination board and has not been published.

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